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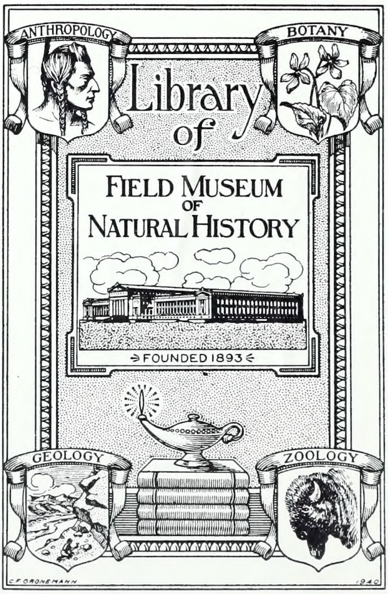

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THE SYSTEMATICS AND EVOLUTION OF THE ORIENTAL COLUBRID SNAKES OF THE GENUS *CALAMARIA*

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INTRODUCTION

The genus *Calamaria*, distributed from southern China and the Riu Kiu Islands southward through the East Indies to the Philippines and Celebes, is one of the two or three most successful genera of colubrids in the eastern Oriental tropics. These highly specialized, burrowing, forest-dwelling snakes are easily recognized as members of a single genus. Very few species of colubrid snakes have as few scale rows (13) as *Calamaria;* none have more extensive fusion of head scales. In this highly restricted morphological framework, no amount of speciation can disguise the generic identity of a form. One result of this homogeneity is that only four generic names have been proposed for the 143 forms named since 1826.

Definition of species limits, however, has been a difficult problem in the past because of the homogeneity of the group and because so few specimens have been available to most workers. Since the last revision (de Rooij, 1917) of a large section of the genus, two enormous collections of a few species have been made at several localities in Java (Kopstein, 1941; de Haas, 1941). These collections housed in the Rijksmuseum van Natuurlijke Historie, Leiden, provide a critical means of evaluating variation.

Without an opportunity to examine these Javanese snakes in our own laboratories, our study would have been seriously hampered. We are, therefore, especially grateful to Drs. L. G. Brongersma and M. Boeseman of the Rijksmuseum for having loaned us these very large collections. The curators of other museums have also been generous and in many cases took the most liberal view of administrative rules in lending us specimens. As a result we were able to see more than 2600 specimens.

We wish to express our thanks to the following colleagues and institutions for permission to study specimens in their collections: Gordon Conway and Chin Phui Kong, Agriculture Department, Tuaran, Sabah; Charles M. Bogert, American Museum of Natural History (AMNH); James E. Bohlke, Academy of Natural Sciences of Philadelphia (ANSP); J. C. Battersby (retired) and Alice G. C. Grandison, British Museum (Natural History) (BMNH); Alan E.

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We are also grateful to Dr. G. B. Rabb, and Dr. T. M. Uzzell for critical comments on various parts of the manuscript. The drawings, charts, and maps were prepared by Miss Marion Pahl, Miss Phyllis Wade, and Miss Janet Wright. The photographs were taken by Mr. H. V. Holdren. The several versions of the manuscript were typed by Mrs. Marion Anderson and Miss Janet Wright.

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CALAMARIA H. Boie

Calamaria H. Boie *in* F. Boie, 1827, Isis, **20**, col. 519 and 539—type species *Calamaria lumbricoidea* Boie by subsequent designation of Brongersma, Inger, and Marx, ms.

Changulia Gray, 1834, Ill. Ind. Zool., **2**, pl. 86, figs. 6–9—type species *Changulia albiventer* Gray by original designation.

Typhlocalamus Gunther, 1872, Proc. Zool. Soc. London, **1872**, p. 589—type species *Typhlocalamus gracillimus* Gunther by original designation.

Keiometopon Taylor, 1962, Univ. Kansas Sci. Bull., **43**, p. 257—type species *Keimetopon booliati* Taylor by original designation.

Application for conservation of the generic name has been made to the International Commission on Zoological Nomenclature (Brongersma, Inger, and Marx, MS).

Habitus vermiform; head not distinct from neck; tail short.

Eye distinct, diameter greater than, equal to, or smaller than eye-mouth distance; rostral rounded; paired prefrontals fused with internasals and in contact with supralabials; frontal 1½ to 8 times width of supraocular; parietal meeting last supralabial; an enlarged paraparietal (Fig. 1); 4 or 5 supralabials, second and third, third, or third and fourth touching eye; nasal single and surrounding nostril; no loreal; a single preocular present or absent; one postocular; no anterior temporal; mental touching or separated from anterior chin shields; 5 infralabials, first two or three touching anterior chin shield; two pairs of chin shields, posterior ones meeting or separated in midline; 3 or 4 gular scales in midline between chin shields and first ventral.

Dorsal scales in 13 longitudinal rows throughout body length; scales smooth; no apical pits; anal single; subcaudals paired.

Posterior vertebrae without hypapophyses; 6 to 12 maxillary teeth, modified (Fig. 3) in most species; palatal and mandibular teeth conical.

This genus can be distinguished from all other snakes on the basis of the combination of the following characters: dorsal scales in 13 rows throughout body; internasals and prefrontals fused; parietal broadly in contact with supralabials.

The genus *Keiometopon* Taylor was based on a single specimen collected in Malaya. Through the courtesy of Dr. E. H. Taylor we have been able to examine the type specimen. It is clearly an anomalous specimen of *Calamaria schlegeli.* The frontal shield is fused with the prefrontals and a median suture runs the length of the dorsal surface of the head. The scales on the side and ventral surface of the head are normal. Several fusions of the longitudinal scale rows occur opposite the first fifteen ventrals. Between the twentieth and the twenty-sixth ventrals the second scale row on each side splits returning the dorsal scale count to thirteen, which number continues to the vent. The maxillary teeth have the characteristic modification of *Calamaria.*

TAXONOMIC PROCEDURE

In establishing taxa and their interrelations, we have adopted the following procedure:

1) examine all characters practically accessible;
2) analyze variation of characters within sympatric samples;
3) correlate all characters within individuals within samples;
4) establish sympatric taxa on basis of (2) and (3);
5) extend analysis of variation to allopatric samples;
6) on basis of (4) and (5) establish limits of species;
7) compare *Calamaria* with other genera of Colubridae to determine distribution of certain characters in the family;
8) on basis of (7) decide which characters of *Calamaria* are primitive (within the genus) and which derived (or advanced);
9) on basis of (5) and (6) establish relations between species (or species groups);
10) on basis of (8), (9), and zoogeographic possibilities, work out phylogeny within the genus.

The validity of the procedure can be tested through examination of the logic and with fresh material. Perhaps the latter is the best test, for in effect by our taxonomy we are making predictions concerning associations of characters in snakes not yet examined.

RECOGNITION OF SPECIES

Starting with large sympatric samples, such as one from Tjikadjang, Java (Table 1), we have examined as many characters as possible and then analyzed the distribution of the total sample with respect to these characters. As shown in Table 1, the sample from Tjikdajang may be treated as two isolated populations (*linnaei* and *lumbricoidea*) that differ in ventral counts (both sexes), subcaudal counts (females), tail ratio (males), supralabials, three aspects of coloration, and ornamentation of hemipenes.

Treated as one population the Tjikadjang sample consists of two clusters of individuals in a multidimensional space generated by the 14 characters. Fragmentation of a species into two such disparate groups at one locality can occur only under very limited circumstances. The separation may be based on age differences. In this case juveniles (less than 200 mm.) and adults (females with large ova) occur within each group, thus eliminating this explanation. The separation could reflect sexual dimorphism, but the table shows both sexes are well represented in each group. Seasonal changes affect some animals profoundly and produce cyclomorphosis, as in *Daphnia* (Brooks, 1946). Seasonal variation does not account for the division in this sample as half of the "*lumbricoidea*" group and all of the "*linnaei*" group were collected in months January–May; the range of variation (Table 1) within the two groups is too narrow for one-half of the "*lumbricoidea*" group to cause the wide gap between the groups.

The only possible explanation remaining for the split in the sample under the single-species hypothesis is polymorphism. Because of the characters used in the analysis (see below), such polymorphism would involve large segments of the genotypes, which in turn increases the possibility of recombinations, crossovers, and hence intermediate phenotypes. As no intermediate phenotypes appear if we consider coloration, ornamentation of hemipenis, number of supralabials, and number of ventrals (which almost certainly have a multiple factor mode of inheritance), the polymorphism explanation can be rejected.

Thus the split single-species hypothesis can be rejected for lack of a sound biological explanation. This hypothesis also runs contrary to all experience with species of snakes. Clearly the only rational interpretation of the correlated distribution of characters in the Tjikadjang sample is that two reproductively isolated populations are involved.

Another large sample, this one from Wonosobo, Java, was analyzed in the same manner (Table 1). In this case three clusters of individuals develop in the multidimensional space. Again the most

TABLE 1.—Analysis of Variation Within Certain Local Samples of *Calamaria*.

	No.		Ventrals		Subcaudals		Tail ratio[1]		Reduction[2]	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
[Tjikadjang, Java]										
linnaei	25	25	132–42	149–59	15–19	8–12	77–95	32–50	4–9	1–7
lumbricoidea	26	30	179–87	197–208	17–21	13–16	63–73	39–55	2–7	1–6
[Wonosobo, Java]										
linnaei	12	19	134–46	150–64	17–22	9–13	82–113	34–53	3–9	1–7
schlegeli	34	54	145–55	162–73	28–33	23–28	120–148	86–109	5–16	8–14
lumbricoidea	2	1	172–75	196	19–21	15	76–78	48	4	2
[Tjibodas, Java]										
linnaei	5	4	142–45	151–61	17–18	8–11	82–89	41–53	3–5	1–3
lumbricoidea	..	1	..	215	..	16	..	43	..	3
modesta	18	25	155–66	165–94	24–28	13–18	97–119	52–65	1–6	2–5
[Mt. Bonthain, S. Celebes]										
acutirostris	11	9	148–62	167–74	20–24	15–17	86–111	57–66	1–6	2–4
curta	1	3	156	156–70	23	15–17	105	67–82	4	5–6
muelleri	17	16	146–55	165–78	18–21	11–15	80–100	41–62	3–8	3–7
[Mt. Kina Balu, North Borneo]										
schlegeli	2	..	134–35	..	44	..	213	..	13	..
lateralis	1	1	146	150	23	16	91	74	16	12
virgulata	3	3	178–83	195–205	18	9–11	70–74	28–36	4–8	1–5
lumbricoidea	7	7	154–65	170–80	23–24	17–19	88–111	70–81	4–8	4–8
grabowskyi	6	5	176–81	180–90	26–29	21–24	93–98	75–82	18–20	12–17
suluensis	2	3	131–36	144–47	18–20	17–20	79–104	67–84	10–14	13–14
griswoldi	4	5	166–79	183–92	16–17	13–16	59–64	48–56	10–13	9–11
modesta	1	3	140	152–54	19	12–13	91	53–55	9	5–7
schmidti	..	2	..	144	..	14	..	75	..	7–8

[1] In terms of thousandths of total length.

[2] Reduction to four dorsal scale rows located in terms of subcaudals from terminal scute.

					Coloration			Maxillary teeth		
	Supra-labials	Pre-ocu-lar[3]	Mental[4]	Frontal ratio	Network on dorsal scale[3]	Dorsal pattern[5]	Ventral pattern	Shape[6]	No.	Miscellaneous
					[Tjikadjang, Java]					
linnaei	4	+	Y	1⅓–2⅕	+	Sp	checkered with black	M	10	calyces smooth[7]
lumbricoidea	5	+	Y	1½–2	0	I	immaculate yellow	M	9–11	calyces papillate
					[Wonosobo, Java]					
linnaei	4	+	Y	1⅓–2	+	Sp	checkered with black	M	10	calyces smooth
schlegeli	5	0	N	3–5	0	I	immaculate yellow	M	9–10	calyces smooth
lumbricoidea	5	+	Y	1⅓–1⅞	0	I	immaculate yellow	M	9–11	calyces papillate
					[Tjibodas, Java]					
linnaei	4	+	Y	1½–2	+	Sp	checkered with black	M	10	calyces smooth
lumbricoidea	5	+	Y	1⅞	0	I	immaculate yellow	M	9–11	calyces papillate
modesta	5	+	N	2–2½	+	Sp	spotted to black	M	6–9	calyces smooth
					[Mt. Bonthain, S. Celebes]					
acutirostris	5	+	Y	2¾–3½	0	I	yellow, spotted with brown	U	10–12	4 gulars
curta	5	+	Y	1⅚–2	+	I	banded, spotted with yellow	U	7	3 gulars
muelleri	5	+	Y	1¾–3	+	Sp	spotted	M	9–11	3 gulars
					[Mt. Kina Balu, North Borneo]					
schlegeli	5	+	N	3½–4	0	I	immaculate yellow	M	9–10	
lateralis	5	+	N	1¾–2	0	St	immaculate black	M	8	
virgulata	5	+	N	2–2½	+	St	yellow, dark laterally	M	8–10	
lumbricoidea	5	+	Y	1½–2	0	I	banded with black	M	9–11	
grabowskyi	5	+	Y	1½–2	+	Sp	spotted to black	M	8–10	
suluensis	5	+	Y	1⅘–2¼	+	Sp	yellow, dark laterally	M	7–8	
griswoldi	5	+	Y	1⅓–1¾	0	St	immaculate yellow	M	9–10	
modesta	5	+	N	2	+	Sp	spotted to black	M	6–8	
schmidti	4	0	N	5–6	0	I	yellow to black	U	6–7	

[3] + = present; 0 = absent. [4] Y = mental touching chin shields; N = mental not touching chin shields.
[5] Sp = spotted; St = striped; I = immaculate. [6] M = modified; U = unmodified. [7] Calyces of hemipenis.

reasonable biological interpretation is that we have isolated populations. Similarly the sample from Tjibodas, Java, consists of three separate populations.

If we combine all three of these local samples, we arrive at four populations, two of which occur at all three localities. These populations differ from one another in more than a half dozen characters. We have considered sympatric populations that differ to this extent to be distinct species.

A similar analysis of the sample from Mount Bonthain, Celebes, yields three populations that differ as much as the Javan populations though not in exactly the same characters. Not mentioned in the table is the peculiar, pointed snout of *acutirostris*. The rostral shield of *acutirostris* does not curve over the dorsal surface of the snout as it does in *curta* and *muelleri* (compare Figs. 19 and 26). The prefrontal meets the first three supralabials of *acutirostris* but only the first two of *curta* and *muelleri*.

The sample from Mount Kina Balu, North Borneo (Table 1) is more complex than the preceding ones. Our analysis shows it to consist of nine species, any two differing in a number of characters. The difference between such pairs does not always involve the same characters. For example, *suluensis* and *schlegeli* males do not differ in ventral counts but do in the relation of mental and chin shields; *schlegeli* and *virgulata* males differ in ventral counts but not in the relation of mental and chin shields. The table does not do justice to some of the differences. Three species are listed as having a striped dorsal pattern; *lateralis* has one broad white stripe, *virgulata* several narrow dark stripes, and *griswoldi* five narrow light stripes on each side.

In analyzing these sympatric groups, we have been striving for a measure of the genotypic divergence associated with genetically determined reproductive isolation. We have assumed that reproductive isolation depends on extensive differentiation of genotypic patterns. It is impossible in our present state of knowledge to speak directly of genes and chromosomes of *Calamaria*. Instead we are obliged to use the phenotype and to assume that it bears approximately the same correspondence to the genotype of *Calamaria* as the phenotype of *Drosophila* bears to its genotype.

Some of the characters used in the preceding analysis of sympatric species involve metamerism (counts of ventrals and subcaudals), some conformation (tail reduction, shape of teeth, frontal ratio, ornamentation of hemipenis), and some chemistry (coloration). Some involve skeleton (teeth), some skin (color and scale proportions), one an accessory reproductive organ, and others (the metameric characters) skeleton, muscles, blood vessels, and nerves. It is unlikely that any simple change in the genetic background of developmental patterns will affect all of these types of characters and tissues in precisely the same way.

The characters mentioned in this section do not exhaust the list of those used in the total work. Nonetheless, they represent a good sampling of the phenotype. We therefore assume that we have also sampled the genotype.

By virtue of their independent existence together, which demonstrates their reproductive isolation, these groups of sympatric species provide a rough standard of the kinds and extent of differences that distinguish species of *Calamaria*. This standard cannot be applied too rigidly, however, for several factors may alter its applicability. For example, differences between sympatric forms may be exaggerated, compared to those distinguishing allopatric forms, by such phenomena as character displacement (Brown and Wilson, 1956). In the matter of degree of difference, we are far from certain that genotypic differences are strictly proportional to phenotypic differences. We cannot say that in the imaginary case of species A, B, and C having ventral counts, respectively of 140–150, 160–170, and 180–190, that the genotypic differences between A and C are twice those between A and B or between B and C. Yet there are probably positive correlations between phenotypic and genotypic differences and between the extent of genotypic difference and reproductive isolation, which is our basic criterion of specific differentiation.

In general we have applied the rough standard derived from the comparison of sympatric species to comparisons of allopatric populations. Despite the limitations of that standard, we can be reasonably sure that allopatric populations differing morphologically to the same extent as sympatric species are at least as different genotypically as are sympatric species.

Serious difficulties arise when allopatric samples are not identical morphologically, yet do not differ as much, or in as many characters, as do the sympatric species listed in Table 1. Every sample of snakes is part of a species. In a revision one must allocate each to a species or run the risk of advancing a classification that does not classify many of the available samples. If one treats all characters as taxonomically equivalent, as advocated by Sneath and Sokal (1962), a decision in many of these cases is impossible without arbitrary action.

We have felt obliged to judge the differences, in such difficult cases, in terms of the characters involved. That is, we have not considered all characters equally significant or equally helpful in assessing potential reproductive isolation, but have instead attributed varying taxonomic significance to each character. We have not graded taxonomic significance in a rigorous fashion such that character *a* has a value of 1, character *b* a value of 2, and so on. Instead, we have adopted a crude ordinal system that in effect states that a difference between samples in character *a* is more likely to reflect genotypic difference of a fundamental sort (i.e., one associated with reproductive isolation) than is a difference in character *b*. This type of weighting is based on a generic-wide analysis of the extent and nature of variation in each character. Such analysis of characters is the subject of the next section.

VARIATION OF CHARACTERS

Relative width of frontal.—The width of the frontal as a multiple of the width of the supraocular has been used in diagnosing species of *Calamaria* for at least seventy years (cf. Boulenger, 1894). Within local samples the ratio of frontal to supraocular width varies, the magnitude of the range of variation usually being about one-half multiple of supraocular width (e.g., 1½ to 2, see Table 1).

Intraspecific variation itself varies with sample size. As the number of specimens increases, the range of variation in the frontal-supraocular ratio does likewise (Table 2). Similarly, as the maximum value of the ratio within a species increases, the range of variation also increases (Table 3). The last result is not surprising since the physically possible magnitude of variation in a wide frontal is greater than that in a narrow one.

TABLE 2.—Frequency Distribution of Species of *Calamaria* with Respect to Sample Size and Range of Variation in Frontal : Supraocular Ratio.

Sample size	Range of variation 1 or more[1]	Total species
2–5	4	13
6–15	4	13
16–40	3	7
41–637	9	11

[1] Multiple of supraocular width. A range of 1 may be 1½–2½, 2⅓–3⅓, etc.

TABLE 3.—Frequency Distribution of Species[1] of *Calamaria* with Respect to Range of Variation in Frontal : Supraocular Ratio and Intraspecific Maxima of the Ratio.

Intraspecific maximum of ratio	Range of variation 1 or more[2]	Total species
under 2	0	2
2–2⅓	0	14
2½–2⅘	4	9
3–3½	10	13
4 or more	6	6

[1] Species with sample size of 1 are omitted.

[2] Multiple of supraocular width. A range of 1 may be 1½–2½, 2⅓–3⅓, etc.

The wide range of intraspecific variation characteristic of the frontal ratio makes interpretation of observed differences between samples difficult. The safest criterion for interspecific variation is absence of overlap in the observed ranges of the species being compared. Some consideration should also be given to sample size. The difference between *schlegeli* and *linnaei* at Wonosobo (Table 1) is an example of reliable interspecific variation; the ranges do not overlap and the samples are large. The difference between *acutirostris* and *curta* at Mount Bonthain (Table 1) probably represents interspecific variation despite the small number of *curta* involved; the gap between the two ranges gives confidence in the decision. We doubt that the same interpretation can be placed on the difference between the Kina Balu samples of *griswoldi* and *suluensis;* the ranges almost overlap and relatively few specimens were examined.

Oculars.—Species of *Calamaria* have one or no preocular and one postocular. Intraspecific variation in ocular count was found in only two species. In one, *schlegeli,* a preocular is almost always present in the populations from Malaya and Singapore, almost always absent in the population from Java, and present or absent in snakes from Borneo and Sumatra. When a preocular is present in a snake from a population characterized by the absence of preoculars, the scale is small.

We examined only three specimens of the second variable species, *lumholtzi.* Two of the three lacked preoculars but the third had a small one.

Labials.—Species of *Calamaria* have either four or five supralabials. The third and fourth labials border the eye in those species having five supralabials, whereas the second and third do when four supralabials are present. The only exception to this rule is *lowi lowi,* which has four supralabials and only the third one bordering the eye in some populations.

Intraspecific variation in supralabial counts is negligible. Of 276 specimens of *lumbricoidea* counted, 270 had the supralabial formula 5(3–4), three had the formula 5(2–3), two had the formula $5\frac{(2\text{–}3)}{(3\text{–}4)}$, and one $\frac{4(2\text{–}3)}{5(3\text{–}4)}$. Of 253 *gervaisi,* 251 had the formula 5(3–4). Of 223 *schlegeli,* 220 had the formula 5(3–4). Of 199 *modesta,* 198 had 5(3–4). Of 178 *linnaei,* 171 had 4(2–3), two had $\frac{4(2\text{–}3)}{5(3\text{–}4)}$, three had $5\frac{(2\text{–}3)}{(3\text{–}4)}$, and two had 5(3–4).

Supralabials, because of the limited intraspecific variation, are useful in distinguishing species.

Infralabials show less interspecific variation than supralabials. Five is the usual number, the first three touching the anterior chin shield. *Calamaria borneensis* invariably has four infralabials of which only the first two touch the anterior chin shield. In *C. lowi* the infralabial formulas are 4(2) or 5(3).

Paraparietals.—All species of *Calamaria* have an enlarged scale or shield along the posterolateral margin of the parietal and behind and slightly above the level of the last supralabial (Fig. 1). This shield, which we call the paraparietal, is usually surrounded by five or six scales counting the parietal and supralabial.

The functional significance of the difference between these counts is obscure, if indeed there is any. Certain specimens of *lumbricoidea* have only four scales bordering the paraparietal; in these specimens the paraparietal is short, squarish, and does not reach the end of the parietal. In other *lumbricoidea,* the paraparietal is oblong as in Fig. 1 and reaches the end of the parietal or slightly beyond. Although the paraparietals of the two snakes shown in Fig. 1 differ in length, species having five scales bordering the paraparietal do not have consistently longer or shorter paraparietals than those with six.

The difference in counts reflects the number of scale rows meeting the paraparietal. The fourth, fifth, and sixth rows always touch the paraparietal. Species in which the third row also meets the paraparietal have six scales bordering that shield.

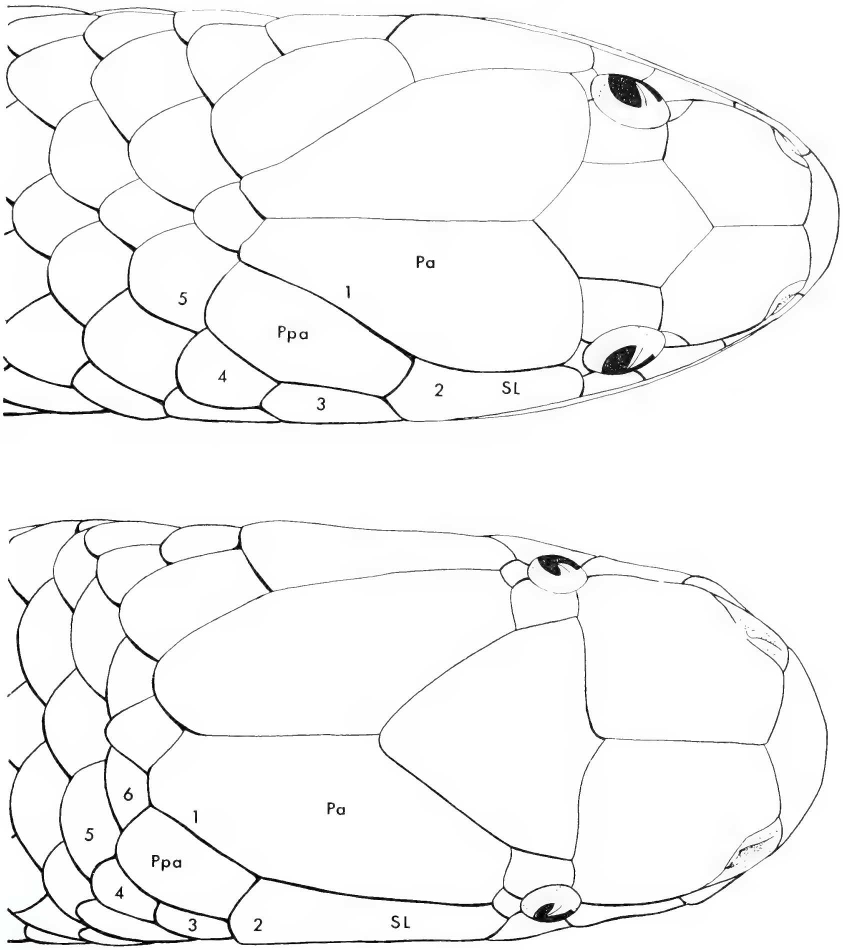

FIG. 1. Position of paraparietal (Ppa) and number of scales surrounding it in *Calamaria buchi* (top) and *C. schmidti* (bottom). Pa=parietal. SL=last supralabial.

Unfortunately, we discovered this variation in scutellation after we had returned part of the material loaned to us. As a result, we have almost no information on this character in some species (e.g., *pavimentata, septentrionalis*) otherwise examined in large numbers. Despite this handicap, the data in Table 4 which lists the larger samples indicate the patterns of variation in this character.

Individual variation within a local population is relatively insignificant. For example, all of 25 *linnaei* from Bogor have counts of

TABLE 4.—Frequency Distribution with Respect to Number of Scales Bordering the Paraparietal in Large Samples of *Calamaria.*

Species	Scales bordering paraparietal						
	$^4/_4$	$^4/_5$	$^5/_5$	$^5/_6$	$^6/_6$	$^6/_7$	$^7/_7$
acutirostris			1	3	24		1
bicolor		1	9				
bitorques			11	1			
borneensis					14		
gervaisi (Manila)		1	94	5			
gervaisi (remainder)		2	155	12	3		
grabowskyi	1	1	18	2			
griswoldi			11				
leucogaster			15	1	1		
linnaei				2	61		1
lowi					34		
lumbricoidea (Philippines)	9	4	5				
lumbricoidea (remainder)		2	151	9	2		
modesta (Borneo)			4				
modesta (remainder)				3	151	1	
muelleri		1	62	1			
nuchalis			1		7		
schlegeli (Sumatra)			1		6		
schlegeli (remainder)			12	1			
suluensis		1	13	1	1		
sumatrana					17		
virgulata (Celebes)					14		
virgulata (Java)					2		
virgulata (Sumatra)			1		1		
virgulata (Borneo)			4				
virgulata (Sulu)			5				
virgulata (Mindanao)			4	1			
virgulata (Palawan)			3				

6/6, all 11 *griswoldi* from Mount Kina Balu have 5/5, and all but 6 per cent of *gervaisi* from Manila have 5/5.

The restriction of local variation gives reliability to the geographic variation observed (Table 4). The extent and sharpness of geographic variation is not the same in all species. *Calamaria gervaisi,* which ranges throughout the Philippine Islands except for Palawan, shows no geographic variation. Although *lumbricoidea* from the Philippine Islands differ in this character from the rest of the species' sample, the frequency distributions overlap considerably. Roughly the same amount of variation occurs in *virgulata,* but differences between populations are sharper.

Our observations indicate that, despite some intraspecific variation and despite limited interspecific variation, this character must be used in any taxonomic work on the genus *Calamaria.*

Relation of mental to anterior chin shields.—The mental shield may touch the anterior chin shields or be separated from them by the first infralabials. We found no intraspecific variation in 31 species; 13

species varied to some extent; nothing can be said about the six species of which we saw only one specimen each. Intraspecific variation (Table 5) may take the form of a relatively rare anomaly as in *linnaei* or *schlegeli*. In *pavimentata, lowi,* and *virgulata* the variation is distinctly geographic. In *alidae* and *modesta* variation, though more frequent than in some species, is not geographic.

TABLE 5.—Frequency Distribution with Respect to the Relation Between the Mental and Anterior Chin Shields in Variable Species of *Calamaria*.

Species	Touching	Separated	Asymmetrical[1]
alidae	2	2	0
bicolor	1	20	0
everetti	0	8	1
grabowskyi	21	0	1
leucogaster	3	33	0
linnaei	222	6	1
lowi (Borneo)	57	0	0
lowi (Malaya)	0	14	0
mecheli	1	6	0
modesta	7	181	7
palavanensis	0	5	1
pavimentata (Laos)	4	0	0
pavimentata (remainder)	2	66	2
schlegeli	1	207	2
virgulata (S. Celebes)	15	0	0
virgulata (N. Celebes)	0	12	0
virgulata (remainder)	0	30	1

[1] One of first infralabials reaching mid-line and thus separating mental from chin shield of that side.

The snakes listed as asymmetrical in Table 5 have been instructive. In these specimens the first infralabial of one side reaches the midline and thereby separates the mental from the chin shield of that side. This variant thus forms an intermediate between two extreme types. Nominate species have been described that differ from others only in the relation of the mental to the chin shields.

Calamaria simalurensis de Rooij, for example, differs from *modesta* only in having the mental touching the anterior chin shields. Yet in the publication (de Rooij, 1917) describing *simalurensis*, the illustration of the holotype of another new species, *elegans* (also from Simalur Island), clearly shows the asymmetrical arrangement. Three other specimens from Simalur we have examined have the mental separated from the chin shields as in Javan *modesta* and agree with *modesta* in all other characters. The large Javan sample (167 specimens) includes six snakes that have the mental touching the chin shields and six that have the asymmetrical pattern. This intermediate arrangement helped us to interpret the variation in this character.

The holotype of *Calamaria schlegeli* differs from the types of *leucocephala* and *agamensis* only in this character. This difference was apparently the reason why Boulenger (1894) separated the last two from *schlegeli.* The holotype is the only specimen of the more than 200 *schlegeli* we have seen having the mental touching the chin shield. The discovery of two snakes having the asymmetrical arrangements supports our decision that this sole difference between *schlegeli* and the two other nominate forms reflects individual rather than interspecific variation.

Table 5 shows that species do differ in this character. The lack of intraspecific variation in 31 species and the low frequency of variants in additional species enable one to use the relation of mental and chin shields as a diagnostic or key character. However, when two samples differ only in this character, probably intraspecific rather than interspecific variation is involved.

Chin shields and gulars.—Every species of *Calamaria* has two well-developed pairs of chin shields. The anterior chin shields are usually larger than the posterior ones and always reach the mid-ventral line. The posterior chin shields also meet in the mid-ventral line in most species, but are separated by a small gular scale in some.

Three or four gulars precede the first ventral in the mid-ventral line. If the posterior chin shields do not meet in the mid-line, invariably there are four gulars in the mid-line. Only one species (*apraeocularis*) having the posterior chin shields meeting in the mid-line has four gulars in the median row.

The relationship of the posterior chin shields to each other and, consequently, the number of median gulars vary geographically in *lumbricoidea* (Table 21). They also vary in *schlegeli,* but the variation is not geographic.

Maxillary teeth.—In our earlier paper on *Calamaria,* we described the distinctive, basally expanded maxillary teeth of many species of *Calamaria.* We have extended our survey to every species in the genus. Although we examined enough specimens of most species to determine the scope of major intraspecific variation, we did not measure enough teeth to permit statistically valid analysis of minor variations in size and shape. This survey was adequate, however, to confirm our earlier finding that there are two sharply different types of maxillary teeth.

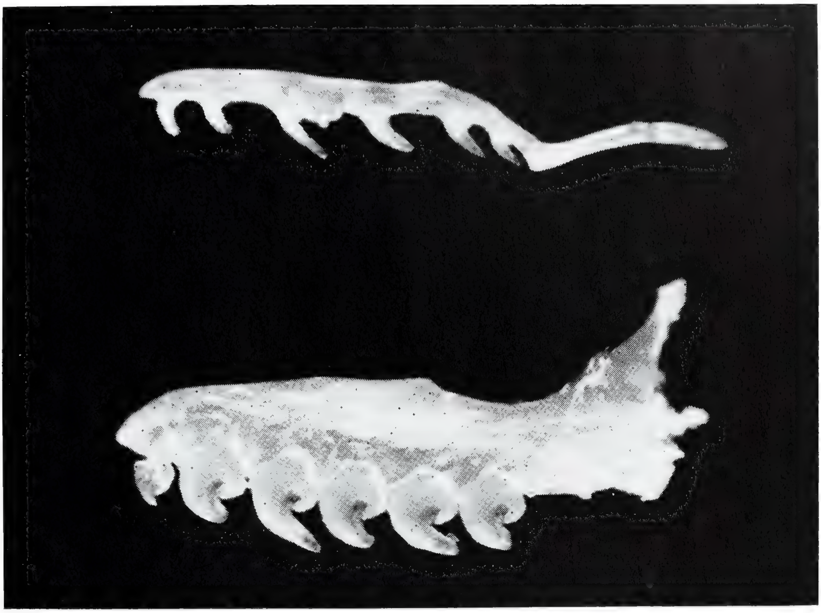

FIG. 2. Maxilla and maxillary teeth of *Calamaria leucogaster* (top) and *C. septentrionalis* (bottom). Length of maxilla in *leucogaster* 5 mm., in *septentrionalis* 3.5 mm.

The peculiarly modified teeth shown in the lower halves of Figures 2 and 3 have bilobed pulp cavities. The pulp cavity in the unmodified, conical type of tooth (upper halves of Figs. 2 and 3) is conical and slightly curved, paralleling the shape of the tooth.

Serial variation is limited to minor changes in size and, in the unmodified dentition, to slight basal thickening of the most posterior teeth. This thickening does not result in a tooth resembling the modified ones. Thus, a snake has but one type of maxillary tooth (Figs. 2 and 3).

Apparently local, individual, and ontogenetic variation do not affect the form of the maxillary teeth. We examined nine *lumbricoidea* from Tjikadjang, Java, and although two were shorter than 200 mm. and two longer than 475 mm., tooth shape in this series was essentially uniform.

The maxillary teeth of *lumbricoidea* from five land masses, of *leucogaster* from three land masses, of *gervaisi* from three, of *virgulata* from four, and of *modesta* from four were examined. We found no intraspecific variation in tooth shape.

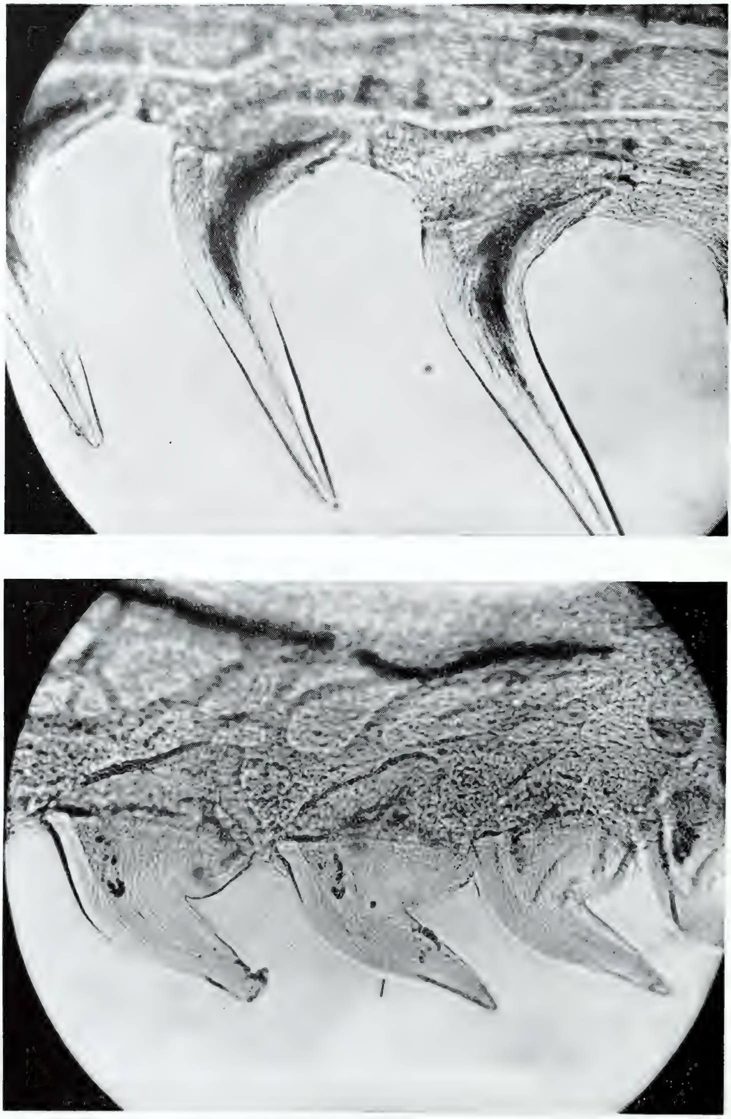

Fig. 3. Unmodified maxillary teeth of *Calamaria acutirostris* (top) and modified ones of *C. linnaei* (bottom).

The number of teeth in a maxilla varies from 6 to 12. In most species the observed range of variation is 2 or 3 (Table 6). Local individual variation in tooth number in certain species may be as great as that over the entire geographic range of most species. For example, *acutirostris* from southern Celebes has 10 to 12 maxillary teeth; *lowi lowi* from western Borneo has 8 to 10. Other species, such as *lumbricoidea,* show almost no local variation. Geographic variation appears in *lowi* and *virgulata.* This form of intraspecific variation may be more common than our limited data indicate.

Sympatric species differ in tooth counts in varying degrees. Bornean specimens of *modesta* have lower counts (6–8) than do Bornean *lumbricoidea* (10). The counts of Bornean *suluensis* and *grabowskyi* overlap but do not coincide. Of the species from southern Celebes, *curta* has distinct counts whereas those of the other three species overlap (Table 6).

The tooth counts are not related to the form of the teeth. The species having unmodified maxillary dentition have 6 to 12 teeth, which is almost identical to but slightly exceeds the range (6 to 11) in species having modified teeth.

All but six species of *Calamaria* have modified maxillary teeth. Because only two types of maxillary teeth occur in this genus, the

TABLE 6.—Variation in Maxillary Dental Counts in Species of *Calamaria.*

		No. of teeth					
		7	8	9	10	11	12
Species	Region	No. of specimens					
curta	southern Celebes	3					
acutirostris	southern Celebes				3	2	3
muelleri	southern Celebes			2	4	2	
nuchalis	southern Celebes			1	2		
lumbricoidea	Philippine Islands				3		
lumbricoidea	Borneo				6		
lumbricoidea	Sumatra			1	7		
lumbricoidea	Java				2	2	
grabowskyi	Borneo		2	2	1		
suluensis	Borneo	2	2				
virgulata	Borneo		2				
virgulata	Java			1			
virgulata	Philippine Islands		1	1			
virgulata	Celebes			2	3		
schlegeli	Borneo			4			
schlegeli	Sumatra			1			
schlegeli	Malaya				3		
schlegeli	Bangka				1		
schlegeli	Java			9	4		
lowi lowi	Borneo		1	2	4		
lowi gimletti	Malaya		2	3			
prakkei	Borneo	5	1				
eiselti	Sumatra				3		
crassa	Sumatra				7		

usefulness of tooth shape in distinguishing between species is limited despite the absence of intraspecific variation. The number of maxillary teeth is potentially of greater value in the definition of species because of the wider intrageneric variation.

The maxillae of species having modified teeth are deeper relative both to the teeth and to the size of the snake. The snakes shown in Figure 2 have teeth of the same length relative to total length. Yet the maximum depth of the maxilla (again relative to total length) of the snake having modified teeth is 1.7 times that of the one having unmodified teeth. The unmodified teeth illustrated are clearly longer relative to the maxilla than are the modified ones.

Similar differences are shown in other specimens. In one of *acutirostris* (447 mm.), which has unmodified teeth, the maximum depth of the maxilla was 42 micrometer units, the length of the longest tooth 45 units. In a *linnaei* (292 mm.), which has modified teeth, the maxilla was 45 units and the tooth 22. In one *lumbricoidea* (393 mm.), which also has modified teeth, the maxilla was 52 units and the tooth 32. The depth of the maxilla relative to total length of these three specimens stand in the relationship of 1.0 to 1.6 to 1.4.

Ventrals.—The generic range in ventral counts is 119 (*joloensis*, ♂) to 304 (*gracillima*, ♀). The maximum counts of most species fall between 146 and 185. The first ventral is preceded by three longitudinal rows of small gular scales and is about as wide as these three rows combined.

Sexual dimorphism in ventral counts is characteristic of *Calamaria*. Females of most species have higher counts than males. Unless intraspecific comparison of the sexes is restricted to specimens collected at one locality, geographic variation complicates the picture. For example, the counts of males of *lumbricoidea* from Tjikadjang, Java completely span the counts of females from Mount Kina Balu although sexual dimorphism is sharp at each locality (Table 7).

Some of the complexities of variation in ventral counts are shown in Table 7 which lists those species represented by at least 17 specimens.

In general, ranges of variation within local populations are relatively narrow, all but three of the 30 examples in Table 7 being less than 16. Neither sample size nor absolute number of ventrals exerts much influence on local ranges of variation (Figs. 4 and 5).

Intraspecific ranges, considering entire species samples, are highly variable. Part of the differences between species in the ranges of

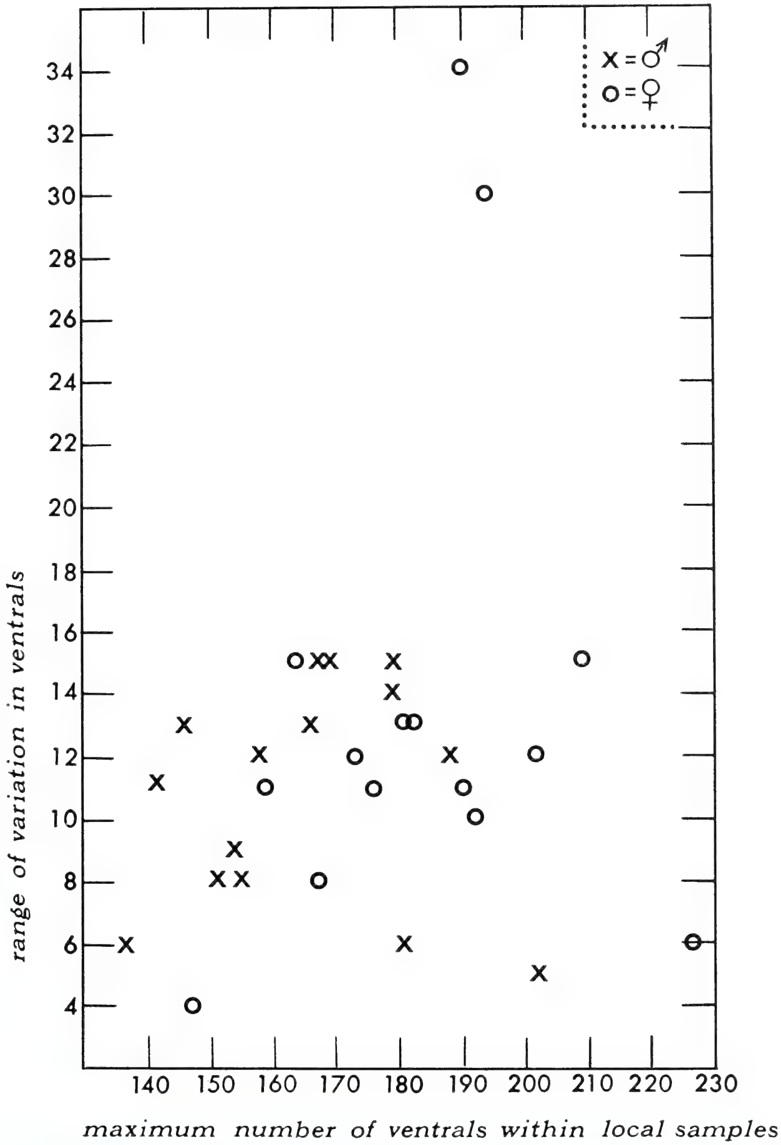

FIG. 4. Relation between maximum number of ventrals and range of variation in ventral counts within local samples of *Calamaria*.

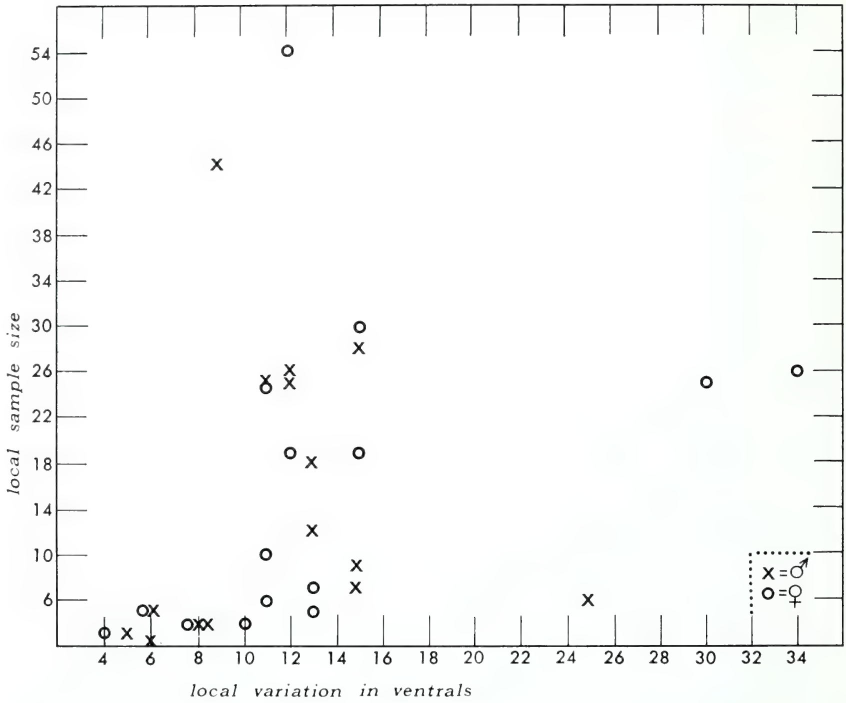

FIG. 5. Relation between local intraspecific variation in ventral counts and local sample size in species of *Calamaria*.

ventral counts can be explained by the maximum individual ventral counts (Fig. 6). It is self-evident that a species having a maximum count of 230 could have, for example, a range of almost 100 ventrals (as in *lumbricoidea*), whereas one having a maximum count of 150 could not.

Sample size has little effect on total intraspecific variation (Fig. 7). The ranges of *linnaei* are about half as extensive as those of *grabowskyi* which is represented by less than a fifth as many specimens (Table 7).

Species of terrestrial snakes distributed in several islands might be expected to show greater ranges of variation than those occurring in only one island because of the geographic isolation of the populations of the first group. However, the ranges of variation in species such as *grabowskyi* and *borneensis,* which are known only from Borneo, may be as great as the ranges of species such as *leucogaster* and *schlegeli,* which occur on three or four land masses including Borneo.

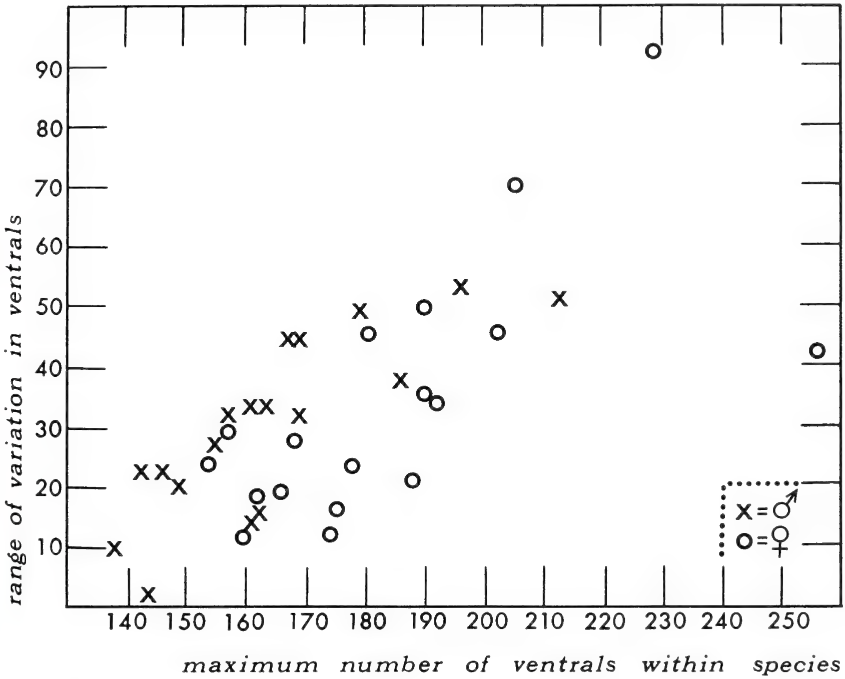

FIG. 6. Relations between maximum number of ventrals and intraspecific ranges of variation in ventral counts in *Calamaria.*

The range of ventral counts in *gervaisi,* which occurs on nine of the Philippine Islands, is no greater than that of *schlegeli* (known from four land masses) and is less than those of *lowi* and *modesta* (each known from three land masses). The range of ventral counts in females of *lumbricoidea* from Borneo is 64, or greater than the range of variation in all other species except *pavimentata.* Thus the fragmentation of the geographic distribution into separate land masses does not affect the range of ventral counts significantly.

Narrow local variation makes it possible to rely on ventral counts for interspecific comparisons, provided the samples being compared are from the same locality (first four lines of Table 7). Interspecific comparisons of ventral counts based on allopatric samples are not reliable because of the wide intraspecific ranges of variation in some species; such interspecific comparisons must be bolstered by evidence from other characters.

Subcaudals.—The observed generic range in these counts is six (*septentrionalis,* ♀) to 44 (*schlegeli,* ♂), the maximum within spe-

Table 7.—Intraspecific Ranges of Variation in Ventral Counts of *Calamaria* in Local and Species-wide Samples.

	Single locality				Entire geographic range			
	Males		Females		Males		Females	
Species	No.	Range	No.	Range	No.	Range	No.	Range
[Mount Kina Balu, Borneo]								
lumbricoidea	7	154–165	7	170–180	132	144–196	116	137–229
grabowskyi	6	176–181	5	180–190	15	150–186	18	164–190
suluensis	2	131–136	3	144–147	6	129–138	13	142–168
griswoldi	4	166–179	5	183–192	6	155–179	5	183–192
[Tjikadjang, Java]								
lumbricoidea	26	179–187	30	197–209	132	144–196	116	137–229
linnaei	25	132–142	25	149–159	75	130–149	95	148–166
[Wonosobo, Java]								
linnaei	12	134–146	19	150–164	75	130–149	95	148–166
schlegeli	44	145–155	54	162–173	102	129–161	115	136–180
[Penang Island]								
schlegeli	4	144–151	4	160–167	102	129–161	115	136–180
[Suisharyo, Formosa]								
pavimentata	4	148–155	10	166–176	37	125–168	50	137–206
[Long Mujan, Borneo]								
borneensis	9	155–169	5	170–182	24	126–169	28	159–192
lowi	3	198–202	5	221–226	20	163–213	28	215–256
[Manila, Luzon]								
gervaisi	25	147–158	26	157–190	81	132–164	101	142–190
[Bandung, Java]								
modesta	28	165–179	19	191–202	97	131–179	76	158–202
[Tjibodas, Java]								
modesta	18	155–166	25	165–194	97	131–179	76	158–202
acutirostris					18	148–161	16	163–174
muelleri					30	129–155	38	155–178
bicolor					12	139–169	6	151–160
sumatrana					6	126–157	11	164–175
melanota					9	121–142	9	131–154
leucogaster					12	126–146	21	129–157
septentrionalis					29	148–166	29	168–188

cies falling between 15 and 30 in 39 species. Intraspecific ranges of variation are variable (Table 8). The patterns of variation are similar to those of ventral counts.

Sexual dimorphism in subcaudal counts (see Table 8) follows the pattern common in the Colubridae. Males have more subcaudals

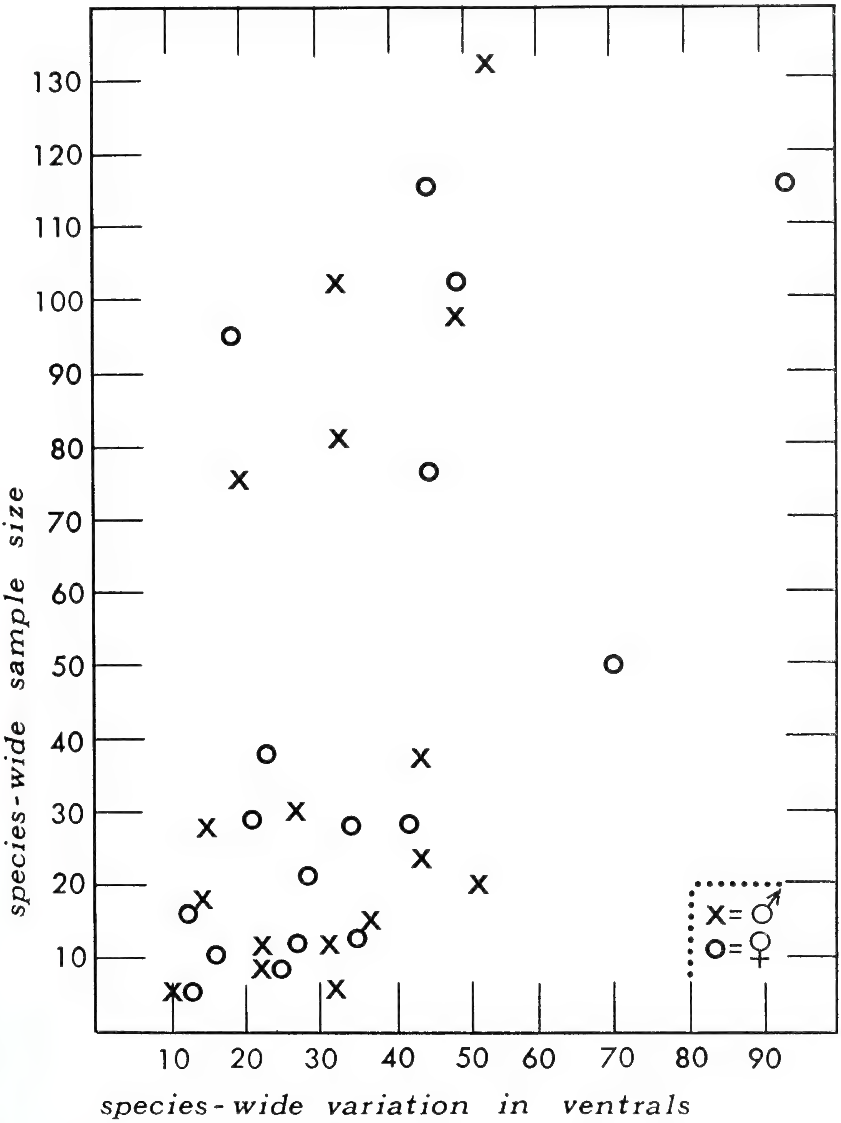

FIG. 7. Relation between intraspecific variation in ventral counts and species-wide sample size in *Calamaria*.

than females in all species of *Calamaria* except possibly *suluensis* (Table 36, p. 128) and *everetti* (p. 133). As in the case of ventral counts comparison of the sexes should be based on specimens from a single locality because of geographic variation. Females of *lumbri-*

TABLE 8.—Intraspecific Ranges of Variation in Subcaudal Counts of *Calamaria* in Local and Species Wide Samples.

	Single locality				Entire geographic range			
	Males		Females		Males		Females	
Species	No.	Range	No.	Range	No.	Range	No.	Range
	[Mount Kina Balu, Borneo]							
lumbricoidea	7	23–24	7	17–19	134	17–27	118	13–21
grabowskyi	6	26–29	5	21–24	15	23–29	18	20–28
suluensis	2	18–20	2	17–20	6	18–20	13	14–26
griswoldi	4	16–17	4	13–16	6	16–18	4	13–16
	[Tjikadjang, Java]							
lumbricoidea	26	17–21	30	13–16	134	17–27	118	13–21
linnaei	25	15–19	25	8–12	74	15–22	95	7–13
	[Wonosobo, Java]							
linnaei	11	17–22	19	9–13	74	15–22	95	7–13
schlegeli	42	28–33	52	23–28	99	25–44	113	19–37
	[Penang Island]							
schlegeli	4	29–32	4	24–25	99	25–44	113	19–37
	[Suisharyo, Formosa]							
pavimentata	4	20–23	10	16–18	38	13–33	50	8–20
	[Long Mujan, Borneo]							
borneensis	8	20–22	5	13–19	24	20–26	28	13–21
lowi	3	19–22	5	12–14	26	14–26	37	10–18
	[Manila, Luzon]							
gervaisi	41	15–19	34	10–14	110	15–21	129	10–18
	[Bandung, Java]							
modesta	31	25–29	19	15–19	100	19–31	79	12–21
	[Tjibodas, Java]							
modesta	14	24–28	18	13–18	100	19–31	79	12–21
acutirostris					18	20–24	16	13–17
bicolor					12	21–28	7	18–21
leucogaster					14	17–26	22	12–19
melanota					9	23–26	9	16–20
muelleri					29	16–21	38	9–15
septentrionalis					28	15–19	30	6–11
sumatrana					6	14–20	11	10–14

coidea from Mount Kina Balu have almost as many subcaudals as males of *lumbricoidea* from Tjikadjang, Java (Table 8), though sexual dimorphism is clear at each locality.

The evidence for lack of dimorphism in *suluensis* and *everetti* is equivocal. At Mount Kina Balu the few males and females seen of *suluensis* had almost identical subcaudal counts, whereas in southeastern Borneo males seem to have slightly higher counts (Table 8). In the case of *everetti*, none of the males came from the localities of the females.

Within local populations the intraspecific range of variation is usually less than six subcaudals. Neither sample size nor maximum number of subcaudals affects the local range of variation (Figs. 8 and 9).

When entire species samples are analyzed, intraspecific ranges increase primarily because of geographic variation, which is relatively common (see Tables 26, 30, 45). Intraspecific ranges at this sampling level vary according to the maximum individual counts within species (Fig. 8); a species such as *schlegeli* (maximum subcaudal count 44) can have a total range of variation of 20 subcaudals whereas a species such as *septentrionalis* (maximum subcaudals 19) cannot. The size of the total species sample had little effect on range of variation (Fig. 9).

Because of narrow local variation, subcaudal counts are helpful in differentiating between sympatric species. Their usefulness in interspecific comparisons when allopatric samples are involved is not as great, though some species are decidedly short-tailed and others long-tailed.

Reduction of the number of dorsal scale rows on the tail.—The number of dorsal scale rows on the tail is reduced to four in most species of *Calamaria*. As in our previous study, we have located the position of the reduction to four rows by means of the subcaudal opposite which it occurs. In Table 9 we have listed the position of the reduction in terms of subcaudals between the level of the reduction and the vent and between the reduction and the terminal scute.

Individual variation is extensive in most species and in both sexes, yet not so extensive as to obscure sex dimorphism and interspecific variation (Table 9).

The position of the reduction to four rows is affected by at least two factors. Whether measured from the vent or from the terminal scute, the position of the reduction is correlated with the total number of subcaudals. It is self-evident that, as the total subcaudal count decreases, the maximum number of subcaudals separating the level of the reduction from either end of the tail must decrease. Yet the total number of subcaudals accounts for only slightly more than half of the variation in position of the reduction (or between 0.39 and 0.82; see Table 10).

The other factor influencing the position of the reduction is tail shape. This influence is reflected in sex dimorphism and in interspecific variation. Males of *Calamaria* are like those of most other snakes in having thicker tails basally than females. This difference is evident in the consistently greater mean distance of the level of the reduction from the vent in males (Table 9). Only four of the 21 means of males are less than 11 subcaudals from the vent and hence in the section of the tail sheathing the hemipenes. By contrast 13 of 21 means of females lie within 11 subcaudals from the vent. Sim-

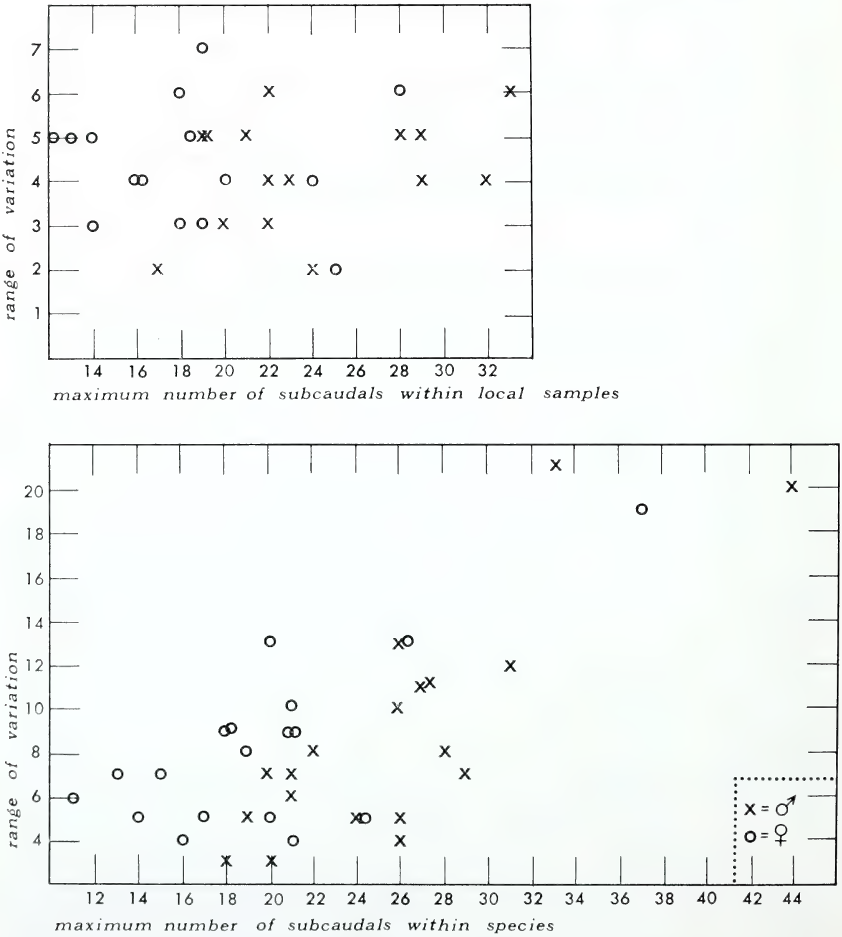

FIG. 8. Relation between intraspecific variation in subcaudal counts and maximum number of subcaudals in local (top) and species-wide samples (bottom) of *Calamaria*.

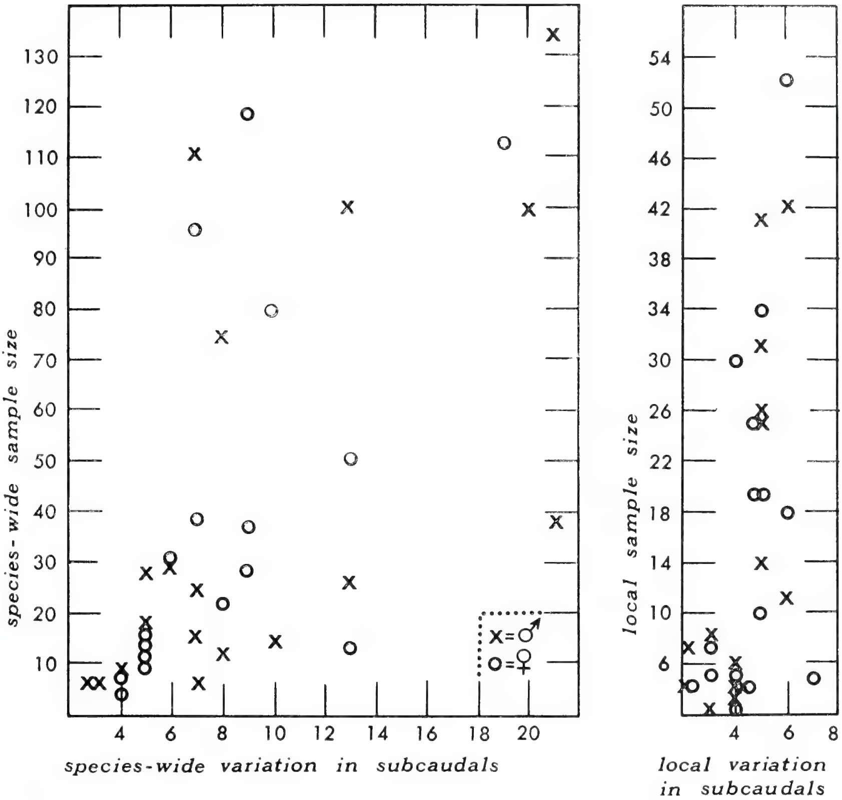

FIG. 9. Relation between intraspecific variation in subcaudal counts and size of species-wide (left) and local (right) samples of *Calamaria*.

ilarly the minimum distance from the vent in the 21 species listed in Table 9 is less in females than in males; the minimum distance in females of all 21 species falls within 10 subcaudals (11 of them within 5 subcaudals) whereas only 14 of the minima of males lie in that range (only three within five subcaudals).

Sex dimorphism in the number of subcaudals between the level of the reduction and the terminal scute is, with few exceptions, not significant statistically or otherwise (Table 9).

The importance of shape in determining the position of the reduction is also shown by interspecific differences. In species having slender tails the reduction takes place much farther from the terminal scute than in thick-tailed species. Males of *septentrionalis*, *linnaei*, and *griswoldi* have approximately the same number of subcaudals

TABLE 9.—Position of the Reduction to Four Dorsal Scale Rows on the Tail of Species of *Calamaria*. Reduction Is Located by Means of Subcaudal Opposite Which It Occurs.

	MALES							FEMALES						
		Subcaudals		Reduction from vent		Reduction from terminal scute			Subcaudals		Reduction from vent		Reduction from terminal scute	
	No.	Range	Mean	Range	Mean	Range	Mean	No.	Range	Mean	Range	Mean	Range	Mean
acutirostris	18	20–24	21.5	15–20	17.9	1–6	3.6	16	13–17	15.2	10–14	12.1	2–6	3.1
bicolor	12	21–28	24.9	7–19	15.5	5–14	9.4	6	18–21	19.7	7–13	9.7	7–12	10.0
borneensis	24	20–26	22.3	10–19	15.6	2–11	6.7	26	13–21	18.2	6–20	13.3	1–10	4.9
gervaisi	110	15–21	17.2	5–14	10.1	4–12	7.2	127	10–18	13.2	3–11	6.8	3–12	6.4
grabowskyi	15	23–29	26.3	4–10	7.7	13–21	18.5	13	20–24	21.8	3–11	6.7	12–17	15.2
griswoldi	6	16–18	16.7	4–6	5.5	10–13	11.2	5	13–16	14.5	3–6	4.6	9–11	10.0
leucogaster	14	17–26	21.2	11–18	13.8	4–13	7.4	22	12–19	15.4	2–14	9.1	3–16	6.3
linnaei	73	15–22	17.5	8–18	12.0	1–9	5.7	91	7–13	10.4	4–11	7.0	1–7	3.5
lowi	20	14–25	20.0	13–21	16.2	0–9	3.8	28	10–18	13.1	6–13	9.4	0–10	3.7
lumbricoidea (all)	134	17–27	21.5	10–25	16.0	2–11	5.3	117	13–21	16.3	6–18	11.7	1–10	4.7
lumbricoidea (Tjikadjang)	34	17–21	19.5	12–19	15.4	2–7	5.0	36	13–16	14.8	8–13	11.1	1–6	4.8
melanota	9	23–26	24.3	16–23	19.4	1–8	4.9	8	16–20	17.6	8–13	11.0	4–9	6.3
modesta	96	19–31	26.3	10–27	22.6	1–9	3.7	75	12–21	16.8	5–18	13.5	1–10	3.2
muelleri	29	16–21	18.5	8–17	13.4	3–8	5.1	38	9–15	12.8	4–11	7.9	2–7	4.8
pavimentata	35	13–33	22.3	6–31	17.4	1–12	4.8	48	8–20	15.2	4–19	11.4	0–8	3.8
septentrionalis	28	15–19	16.5	15–19	16.5	0	0	31	6–11	9.1	6–11	9.1	0	0
s. schlegeli	48	25–44	33.3	6–31	16.8	9–25	16.3	46	19–37	26.5	5–21	10.7	7–25	15.7
s. cuvieri	42	28–33	31.0	15–26	19.7	5–16	11.3	52	23–28	24.9	10–18	14.1	8–17	10.7
suluensis	6	18–20	18.8	7–12	9.3	7–14	10.5	13	14–26	19.0	2–16	7.2	9–19	12.3
sumatrana	6	14–20	17.7	8–16	12.5	3–8	5.2	11	10–14	12.0	7–11	8.7	0–5	3.3
virgulata	20	16–30	19.3	8–26	14.3	0–9	5.2	38	8–16	11.1	5–13	7.6	0–5	3.5

(means 16.5–17.5). In *septentrionalis* (Fig. 10A) the tail does not taper and six scale rows reach the terminal scute. The tail of *linnaei* is slightly tapered and the mean number of subcaudals between the reduction rows and the terminal scute is 5.7 (33 per cent of the

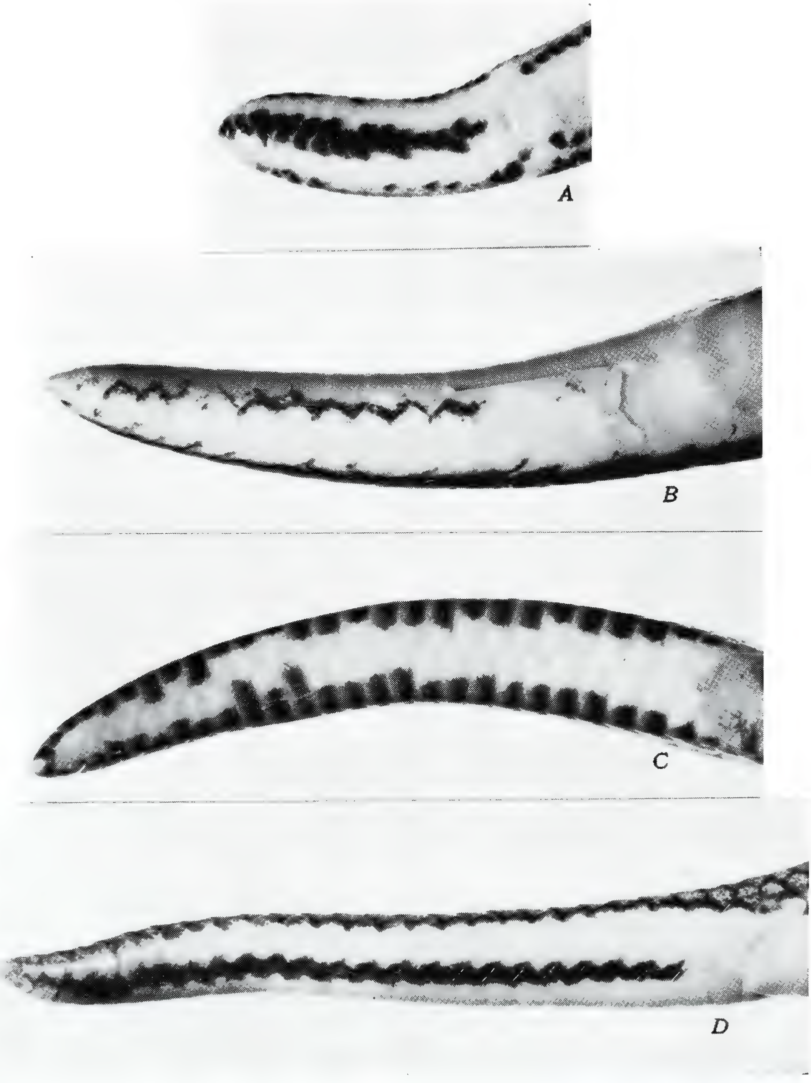

FIG. 10. Ventral views of tails in males of *Calamaria septentrionalis* (A), *C. griswoldi* (B), *C. modesta* (C), and *C. grabowskyi* (D).

TABLE 10.—Correlation Between Total Number of Subcaudals and Position of Reduction to Four Dorsal Scale Rows in Species of *Calamaria.*

	Reduction from vent		Reduction from terminal scute	
	r	P	r	P
Males	+0.49	0.02	+0.56	<0.01
Females	+0.39	>0.10	+0.82	<0.001

total). The tail of *griswoldi* (Fig. 10B) is one of the most slender in the genus and the reduction is 11.2 subcaudals (67 per cent) from the terminal scute. Males of *modesta* and *grabowskyi* have equally long tails (means of subcaudals 26.3 in both), but that of *grabowskyi* (Fig. 10D) is tapered near the base and that of *modesta* (Fig. 10C) only near the tip. The mean position of the reduction in *grabowskyi* males is 18.5 subcaudals (70 per cent of the total) from the terminal scute and 3.7 (14 per cent of the total) in males of *modesta.*

Thus despite individual variation and sexual dimorphism, the position of the reduction to four rows can be used as a valid taxonomic character and in some cases helps in distinguishing between species. Because sexual dimorphism in the number of subcaudals between the reduction and the terminal scute is less pronounced than in the number between the vent and reduction, we have given the position of the reduction relative to the end of the tail in the descriptions of species.

Hemipenis and cloaca.—The retracted hemipenes of slightly more than half of the species were examined (Table 11). The material available was not sufficient for adequate sampling of each species. We dissected the hemipenis of a single male in nine species, of two males in 11 species, of three males in four species, of four males in two species, of five males in one, of 20 males in one, and of 46 males in one. Our analysis of variation is, therefore, of limited value.

TABLE 11.—Frequency Distribution of Species of *Calamaria* with Respect to Form of Hemipenis.

	Body of hemipenis			
	Forked	Non-forked	Forked or non-forked	Unknown
Calyces				
Smooth	17	1		
Papillate	6	1		
Smooth or papillate	1		1	
Unknown	2			21

The most common forms of individual variation involve the position of the fork and the length of the hemipenis. The fork of the retracted hemipenis usually lies opposite the fourth to sixth subcaudal. In 24 males of *lumbricoidea*, the fork was opposite the second subcaudal in two specimens, opposite the third in three, the fourth in 11, the fifth in seven, and the sixth in one. In 12 males of *schlegeli* the fork lay opposite the fourth subcaudal in six, the fifth in five, and the sixth in one. Similar variation occurs in 14 of the 16 other species which have forked hemipenes and of which we examined two or more males.

TABLE 12.—Relations of Length of Hemipenis to Total Number of Subcaudals in Two Species of *Calamaria*.

C. lumbricoidea

	Total number of subcaudals								
End of hemipenis[1]	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*
	Number of specimens								
6	1			1					
7				1					
8			1	3	1		1		
9			3	2	2	2			
10			1	3	1	1		1	
11									1

C. schlegeli

	Total number of subcaudals								
	27	*28*	*29*	*30*	*31*	*34*	*39*	*40*	*42*
	Number of specimens								
7		1							
8				1	1				
9		2	1			1		1	
10							1	1	1
11	1								

[1] Determined by subcaudal opposite which retractor muscle inserts on hemipenis.

We have measured the length of the hemipenis in terms of subcaudals, letting the insertion of the retractor muscle mark the end of the hemipenis. The retractor may insert as close to the vent as the sixth subcaudal and as far as the fourteenth; in most males examined the insertion is opposite the eighth to tenth.

In the two large series examined, *lumbricoidea* and *schlegeli*, the length of the hemipenis varies. But that variation bears little relation to tail length as measured in terms of subcaudals (Table 12). Similar minor variation occurs in other species.

What may be called major, in contrast to the preceding minor, variation appears in *suluensis* and *lumbricoidea.* The calyces of one *suluensis* male are smooth-edged, those in a second papillate. The hemipenes of *lumbricoidea* are simple (non-forked) with smooth-edged calyces, forked with smooth calyces, or forked with papillate calyces. These variants are geographically localized (Inger and Marx, 1962; see also p. 85 of this paper).

As we examined at most two males in 20 of the 29 species dissected, the true extent of major intraspecific variation in hemipenes cannot be evaluated from our data. Intraspecific variation as striking as that of *lumbricoidea* should not be expected in every species, for only minor variation was found in 20 males of *schlegeli* from all parts of that species' wide range.

Most species of *Calamaria* have deeply forked hemipenes having smooth-edged calyces (Table 11). Although the characteristics of many of the species in the table are based on the dissection of one or two males, the previous generalization seems valid. Even if major intraspecific variation is much more common than our data indicate, it is unlikely that we would have found such a high proportion of snakes falling in one cell of Table 11—provided that our selection of specimens for dissection was random with respect to hemipenial form. As we found no ontogenetic variation in hemipenes and as we could not know the form of the hemipenis prior to dissection, randomness in our selection was assured.

We dissected two males of each of the two species characterized by non-forked hemipenes and two or three males of four species characterized by papillate hemipenes. Despite the small samples involved, we believe that much of the interspecific variation indicated in Table 11 will be substantiated by future work.

The cloacas of females have three general forms (Inger and Marx, 1962). Cloacas called bulbous have oviducts opening into the chamber posterior to the anterior wall of the cloaca. If the anterior end of the cloaca has an indentation and the oviducts open posteriorly, the cloaca is called cardioid. A bilobed cloaca has the oviducts opening into the anterior ends of short cloacal lobes.

Females of 20 species were dissected. We examined one female of each of seven species, two of each of 10 species, three of one, four of one, and 27 of one (*lumbricoidea*). Only four of the two-specimen samples show no variation. The cloacas of the other multi-specimen samples fall in at least two categories.

Variation in cloacal form is apparently not related to stage of the reproductive cycle (Inger and Marx, 1962). Possibly the shape of the cloaca is transitory and modified by differential contraction of muscles.

In view of the wide intraspecific variation, we have not utilized cloacal form in our taxonomic decisions.

Thickness.—Species of *Calamaria* clearly differ in body thickness. Great variation in quality of preservation made it impractical to measure the thickness of the body directly. The only satisfactory method of determining bulk was by water displacement which gave us the volume of each animal. Obviously shrunken and broken animals were not used. Unfortunately these measurements were not made until relatively late in our study after a good part of the borrowed material had been returned.

A graduated cylinder was partly filled so that the meniscus was at a given line. A snake was submerged and the increase in volume (to the nearest 0.5 ml.) gave us the volume of the snake. The volume was divided by the total length of the individual giving the volume per millimeter of length. This measure is an index of thickness.

Despite the limitations of small samples, these measurements give clear indication of ontogenetic changes in body thickness, weaker indications of sexual dimorphism, and good indications of interspecific variation (Fig. 11).

We have made volume measurements for 43 species (Table 13); 21 species are represented by enough measurements to indicate at least the pattern of individual variation. Eighteen of the 21 show ontogenetic variation clearly. Each of these eighteen species shows increase in the volume per millimeter of total length as total length increases. The three species that do not show clear ontogenetic change in this character are *leucogaster, lowi,* and *sumatrana;* the last two species are slender and the first is moderate in thickness.

In *lumbricoidea, gervaisi, schlegeli,* and *virgulata* the males seem to be somewhat bulkier than females of corresponding lengths. Even in these species, however, the data are too few to substantiate this relationship. Differences between species in thickness show up with even quick visual examination. For example, *eiselti* is several times the diameter of *lowi;* these two species represent extremes of thickness in this genus (Fig. 11). The results of visual inspection are confirmed by our measurements of volume (Table 13). Even relatively subtle differences between species (e.g., *eiselti* vs. *crassa* or *lumbricoidea*) can be detected by these measurements.

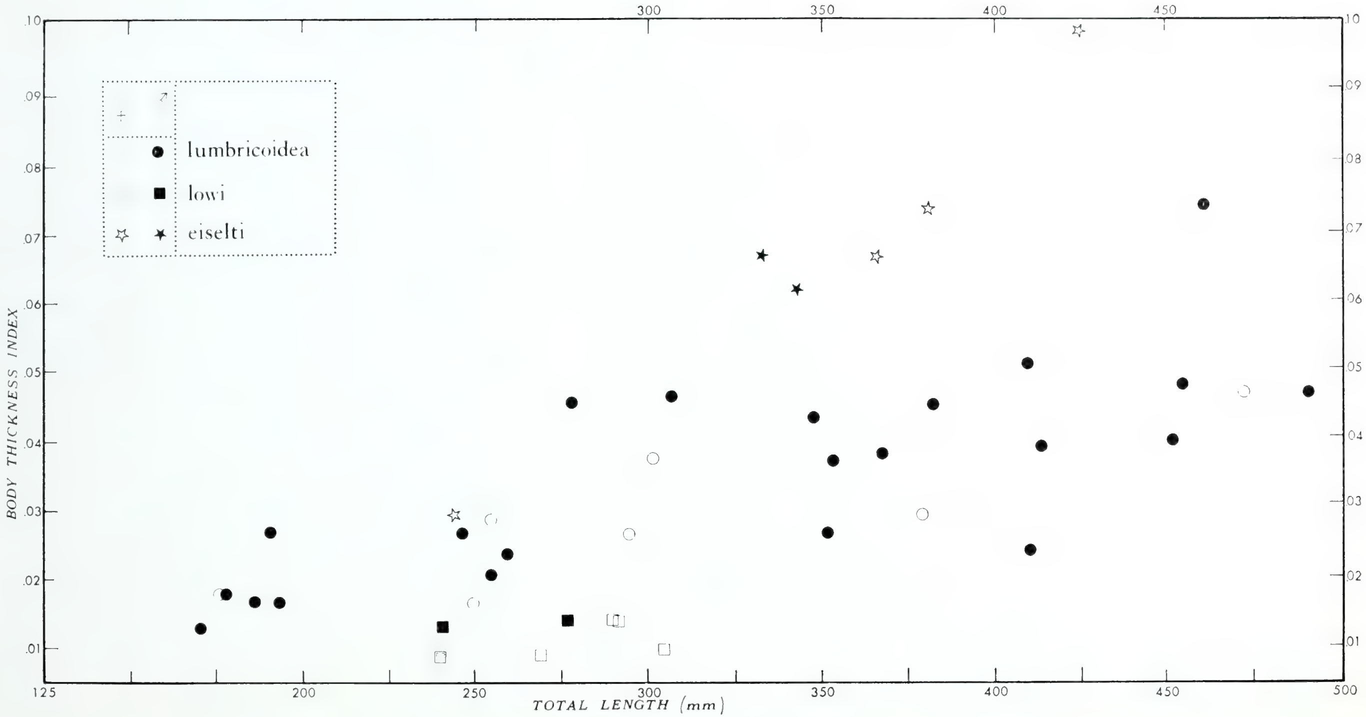

FIG. 11. Thickness of body (ml./mm.) in three species of *Calamaria*.

TABLE 13.—Body Volume and Ratio of Volume to Total Length and Numbers of Ventrals and Subcaudals in *Calamaria.*

Museum number	Locality	Sex	Total Length mm.	Vol. ml.	Vol./TL ml./mm.	Ventrals	Subcaudals
lowi							
SM "14"	Borneo	♀	238	2	0.008	226	14
CNHM 109974	"	♀	238	2	0.008	225	16
CNHM 72373	"	♂	239	3	0.013	202	20
CNHM 129001	"	♀	268	2.5	0.009	238	18
CNHM 109975	"	♂	276	4	0.014	196	24
CNHM 129002	"	♀	289	4	0.014	246	15
CNHM 109976	"	♀	291	4	0.014	233	12
CNHM 129003	"	♀	304	3	0.010	228	14
alidae							
NHMW 16996	Sumatra	♂	254	3	0.012	203	27
apraeocularis							
MCZ 25265	Celebes	♂	148	1	0.007	178	18
MCZ 25300	"	♀	237	3	0.013	220	10
forcarti							
NMB 8958	Nias	♂	216	2	0.009	176	30
ZMA 10073	"	♀	235	2	0.009	200	16
NHMW 16710	Sumatra	♂	239	2	0.008	177	30
buchi							
CNHM 71697	Indo-China	♀	389	8	0.021	221	13
pavimentata							
CNHM 100869	Tonkin	♀	268	3	0.011	186	16
CNHM 11528	Annam	♂	244	5	0.012	160	21
virgulata							
ZMA 10240	Sumatra	♂	100	0.75	0.008	195	16
RMNH —	Celebes	♀	150	1.5	0.010	180	10
RMNH —	"	♀	173	2.5	0.014	182	10
SU 22405	Mindanao	♂	193	2	0.010	227	20
RMNH —	Celebes	♂	195	3	0.015	160	19
RMNH —	"	♀	219	3	0.014	182	10
RMNH —	"	♀	225	3	0.013	192	11
NHMW 16695	Java	♂	237	4	0.017	197	17
NMS 4	Celebes	♀	254	4	0.016	208	11
NMS 4	"	♀	257	4	0.016	208	13
CNHM 63571	Borneo	♀	258	4	0.016	205	10
NHMW 16716:2	Celebes	♀	271	5	0.018	216	12
RMNH —	"	♀	273	6	0.023	194	10
RMNH 39	Java	♂	283	6	0.021	189	19
NHMW 16716:1	Celebes	♂	286	5.5	0.019	192	18
MHNP 5780	no data	♀	307	4.5	0.015	236	12
SNG 19441	Celebes	♀	336	6	0.018	209	12
joloensis							
CAS 60901	Jolo	♂	144	1.5	0.010	119	13
boesemani							
GM 3230	Celebes	♀	116	1	0.009	170	16

TABLE 13 (cont.)

Museum number	Locality	Sex	Total Length, mm.	Vol. ml.	Vol./TL ml./mm.	Ven- trals	Sub- caudals
brongersmai							
GM 3229	Celebes	♂	225	4	0.018	155	18
everetti							
RMNH ——	Borneo	♂	144	2	0.014	157	20
CNHM 63572	"	♂	168	1.5	0.009	151	20
BM 1902	"	♀	187	2	0.011	152	25
CNHM 109971	"	♀	208	2	0.010	153	24
javanica							
CNHM 109791	Billiton	♀	169	2	0.012	168	10
lateralis							
MCZ 43582	Borneo	♀	190	2	0.011	150	16
sumatrana							
MCG 30382	Sumatra	♂	168	3	0.018	126	14
ZMA 10238	"	♂	169	2.5	0.015	130	16
ZMH 3996	"	♂	174	2.5	0.014	149	18
AMNH 2873	"	♀	184	1.75	0.010	165	11
ZMH 3996	"	♀	200	2.5	0.013	167	11
RMNH 4860	"	♀	208	2	0.010	173	12
ZMH 2466	"	♂	222	3	0.014	157	19
ZMA 10237	"	♀	227	4	0.018	164	10
ZMH 2307	"	♀	234	3.5	0.015	174	13
abstrusa							
ZMB 5986	no data	♂	162	1.75	0.011	130	24
ZMB 5986	"	♂	162	1.75	0.011	129	24
BM 64.4.7.11	Sumatra?	♀	209	2.5	0.012	152	14
borneensis							
CNHM 109973	Borneo	♂	209	3	0.014	138	22
SMNS 4584	"	♀	210	3	0.014	175	18
CNHM 76295	"	♀	228	3	0.013	171	20
SMNS 4584	"	♀	244	4	0.016	176	19
CNHM 72372	"	♂	275	6	0.022	159	22
CNHM 109972	"	♀	353	11	0.031	177	17
suluensis							
SMNS 34.98	Borneo	♀	109	1	0.009	147	14
RMNH ——	"	♀	165	2	0.012	142	16
RMNH ——	"	♀	190	3	0.016	158	16
MHNP 57-812	"	♂	203	3	0.015	129	18
NHMW 16708:2	"	♂	221	4.25	0.019	138	20
ZMH 4212	"	♂	227	4.5	0.020	133	18
NMS 146.17	"	♀	252	5	0.020	147	17
NHMW 16708:1	"	♀	259	6.75	0.026	154	16
NHMW 16708:3	"	♀	264	6	0.023	161	15
CNHM 76294	"	♀	287	8	0.028	164	26
palavanensis							
BM 94.6.30.51	Palawan	♀	134	1	0.007	178	18
CAS 62151	"	♂	280	6	0.021	174	25
BM 94.6.30.50	"	♀	323	8	0.025	180	16
gervaisi							
SU 17931	Negros	♀	111	1	0.009	170	11
SU 18229	Cebu	♂	120	1	0.008	149	18

TABLE 13 (cont.)

Museum number	Locality	Sex	Total Length, mm.	Vol. ml.	Vol./TL ml./mm.	Ventrals	Subcaudals
CM 2530	Luzon	♀	135	1	0.007	162	12
SU 19874	Negros	♂	149	2	0.013	159	18
CAS 60471	Basilan	♂	170	2	0.012	133	17
CNHM 53377	Mindanao	♂	179	2	0.011	145	19
CM 2470	Luzon	♂	186	2	0.011	153	18
CM 2540	”	♂	186	2.5	0.013	146	16
MCZ 37699	Mindoro	♀	190	2	0.011	172	18
MCZ 25775	Polillo	♀	191	2	0.010	148	15
CM 2485	Luzon	♂	196	3	0.015	155	16
SU 17929	Negros	♂	199	4	0.020	154	17
CNHM 96620	Mindanao	♂	204	4	0.020	147	21
SU 18910	Negros	♂	210	3	0.014	148	18
CM 2537	Luzon	♀	245	5	0.020	160	15
CNHM 53380	Mindanao	♀	258	6	0.023	150	14
MCZ 25752	Tablas	♀	262	6	0.023	163	13
CM 2538	Luzon	♀	263	6	0.023	169	11
SU 15965	Panay	♀	277	6	0.022	168	14
SU 15963	”	♀	281	8.5	0.030	177	13
SU 15947	Negros	♀	321	8	0.025	177	14
nuchalis							
USNM 61201	Celebes	♂	123	1	0.008	146	20
RMNH —	”	♂	184	3	0.016	142	20
RMNH 8382	”	♂	195	5	0.026	133	14
MCZ 45486	”	♂	200	4	0.020	145	20
NHMW 16715	”	♀	249	4	0.016	156	9
RMNH —	”	♂	280	8	0.029	143	19
USNM 61193	”	♂	294	10	0.034	145	19
leucogaster							
RMNH —	Sumatra	♀	151	2.25	0.015	126	18
RMNH —	Borneo	♀	162	1	0.006	147	18
RMNH —	Sumatra	♀	177	5	0.028	127	17
CNHM 71598	Borneo	♀	195	5	0.026	148	18
RMNH —	Sumatra	♂	198	4	0.020	146	13
SMNS 4585	Borneo	♀	205	4	0.020	151	15
RMNH 3994	Sumatra	♀	223	4	0.018	143	14
curta							
MCZ 25302	Celebes	♀	195	3	0.015	170	15
MCZ 25301	”	♀	280	8	0.029	156	17
septentrionalis							
CNHM 7141	China	♂	168	3.5	0.021	160	18
ZSBS 169/47	”	♀	263	6.25	0.024	178	8
CNHM 7140	”	♀	277	8	0.029	180	11
CNHM 7139	”	♀	342	16	0.047	179	10
döderleini							
MZUS —	Sumatra	♂	288	11	0.038	163	20
schlegeli							
ZSBS 1933/0	Borneo	♀	163	2	0.012	148	24
NHMW 16712:6	Sumatra	♀	189	3	0.016	152	22
CNHM 121033	Java	♂	198	3.5	0.018	146	31
SMNS 4586	Borneo	♂	255	6	0.024	129	30
NHMW 16712:3	Sumatra	♀	275	7	0.025	152	22
NHMW 16696:1	Java	♂	283	7.5	0.027	159	29
NHMW 16712:2	Sumatra	♂	287	8	0.028	138	27
CNHM 121039	Java	♀	317	7	0.022	169	26
MHNP 4417	Billiton	♂	326	8.5	0.026	135	34

TABLE 13 (cont.)

Museum number	Locality	Sex	Total Length, mm.	Vol. ml.	Vol./TL ml./mm.	Ven-trals	Sub-caudals
griswoldi							
NMS —	Borneo	♂	236	4	0.017	166	16
CNHM 72434	"	♂	334	13	0.039	170	17
USNM 134114	"	♀	376	9	0.024	190	14
NMS 18949	"	♂	379	14	0.037	171	16
MCZ 43580	"	♀	488	18	0.037	186	13
grabowskyi							
CNHM 76293	Borneo	♂	182	2	0.011	186	28
NHMW 16998	"	♂	259	6	0.023	150	23
RMNH —	"	♂	287	8	0.028	160	25
RMNH —	"	♂	307	9	0.029	162	24
MCZ 43573	"	♂	316	8	0.025	176	27
ZMA 10230	"	♀	340	10	0.029	180	22
NHMW 16693	"	♀	355	14	0.039	168	21
MHNP 89–192	"	♂	362	11	0.030	181	28
MHNP 89–191	"	♀	388	10	0.026	189	21
RMNH 568	"	♀	451	28	0.062	190	20
ceramensis							
CNHM 83464	Ceram	♀	266	7	0.026	154	19
ZSBS 947/20	"	♀	301	11	0.037	165	20
lautensis							
RMNH 4716B	Kokos Ids.	♂	215	6	0.028	123	24
modesta							
MHNP 3299	Java	♀	155	2	0.013	192	18
ZSBS 1935/0	"	♀	201	3	0.015	174	21
ZSBS 2635/0	"	♀	224	3.5	0.016	199	19
ZSBS 2646/0	"	♂	269	8	0.030	154	31
ZSBS 2646/0	"	♀	269	7	0.026	166	21
ZSBS 1934/0	"	♂	286	7	0.024	177	26
ZSBS 2646/0	"	♂	304	11	0.036	154	29
ZSBS 2675/0	"	♀	319	9	0.028	173	18
CNHM 83164	"	♂	343	12	0.035	162	25
ZSBS 2675/0	"	♂	352	12	0.034	171	21
bicolor							
SM "164"	Borneo	♂	164	2	0.012	167	23
NHMW 16997:2	"	♂	178	3	0.017	139	22
MCG 748.36	"	♀	181	4	0.022	159	21
RMNH 68	"	♂	281	7	0.025	152	24
RMNH 1678	"	♂	284	9	0.032	145	21
RMNH —	"	♂	311	10	0.032	142	26
RMNH 10542	"	♀	335	14	0.042	156	20
SM Cd.5.26.7a	"	♀	391	21	0.054	159	20
muelleri							
MCZ 25332	Celebes	♀	146	1	0.007	171	13
NHMW 16692:7	"	♀	208	3	0.014	165	13
USNM 120813	"	♂	214	4.5	0.021	152	18
ZMB 15635	"	♀	218	4	0.018	170	13
MCZ 25322	"	♂	235	6.5	0.028	148	18
SNG 19443	"	♀	242	8	0.033	158	13
SNG 19442	"	♂	254	8	0.031	141	23
MCZ 25317	"	♀	298	8.5	0.029	169	14
MCZ 25315	"	♀	320	9	0.028	172	14
ZMB 13946	"	♀	355	15	0.042	167	12

TABLE 13 (cont.)

Museum number	Locality	Sex	Total Length, mm.	Vol. ml.	Vol./TL ml./mm.	Ventrals	Subcaudals
hilleniusi							
ZMA 10078	Borneo	♂	317	13	0.041	155	18
SM "1"	"	♀	368	19	0.052	154	16
acutirostris							
NHMW 13713:11	Celebes	♂	138	2	0.013	151	21
NHMW 13713:10	"	♀	150	2	0.013	166	14
NHMW 13713:7	"	♂	173	5	0.029	152	21
NHMW 13713:9	"	♂	193	4	0.021	153	21
NHMW 13713:5	"	♀	291	14	0.048	167	16
NHMW 13713:3	"	♂	296	14	0.047	151	21
NHMW 13713:6	"	♀	330	14	0.042	165	14
NHMW 13713:1	"	♂	341	24	0.070	152	21
NHMW 13713:4	"	♀	370	20	0.054	163	13
NHMW 13713:2	"	♀	447	18	0.040	163	15
albiventer							
CAS 14940	Singapore	♀	233	6	0.026	158	15
crassa							
NHMW 16994	Sumatra	♂	131	2	0.015	136	21
RMNH —	"	♂	168	2	0.012	154	27
RMNH 34	"	♀	227	5	0.022	164	15
RMNH 34	"	♀	330	13	0.039	158	14
RMNH 34	"	♀	333	14	0.042	163	15
ZMB 5229	"	♀	334	13	0.039	162	17
RMNH 34	"	♂	342	16	0.047	150	28
RMNH 34	"	♀	372	19	0.051	162	14
melanota							
ZSBS 2039/0	Borneo	♂	182	4.5	0.025	125	24
ZSBS 2039/0	"	♂	189	4	0.021	123	23
SMNS 4529	"	♀	202	3	0.015	148	16
RMNH 1152	"	♀	218	6	0.028	131	18
CNHM 109964	"	♂	230	6	0.026	133	24
lumbricoidea							
NHMW 16992:2–3	Borneo	♂	170	2	0.012	146	21
NHMW 16992:2–3	"	♀	176	3	0.017	160	16
NMS —	Malaya	♂	177	3	0.017	156	22
RMNH 932	Java	♂	186	3	0.016	185	19
SMNS 3497	Borneo	♂	190	5	0.026	164	21
RMNH —	Sumatra	♂	193	3	0.016	162	23
RMNH 4865	Nias	♂	246	6	0.024	149	22
NMS —	Malaya	♀	249	4	0.016	175	16
RMNH 1264	Java	♀	254	7	0.028	203	14
CAS 15289	Mindanao	♂	254	5	0.020	167	22
ZMA 10234	Nias	♂	259	6	0.023	153	20
RMNH 5806	Sumatra	♂	277	12.5	0.045	162	19
NMS 1932	Malaya	♀	294	7.5	0.026	169	18
MCZ 20971	Sumatra	♀	301	11	0.037	179	16
RMNH 5806	"	♂	306	14	0.046	165	22
MCZ 43568	Borneo	♂	347	15	0.043	157	23
ZMH 2466	Sumatra	♂	351	9	0.026	164	21
RMNH 5806	"	♂	353	13	0.037	165	24
NMS —	Malaya	♂	367	14	0.038	165	26
NHMW 16700:1	Sumatra	♀	379	11	0.029	192	16
ZMB 13110	Borneo	♂	382	17	0.045	163	19

TABLE 13 (cont.)

Museum number	Locality	Sex	Total Length, mm.	Vol. ml.	Vol./TL ml./mm.	Ventrals	Subcaudals
RMNH 618	Java	♂	409	21	0.051	182	19
NHMW 16701:2	Sumatra	♂	410	10	0.024	191	22
NMS —	Malaya	♂	413	16	0.039	162	22
RMNH 831	Java	♂	451	18	0.040	187	19
NMS —	Malaya	♂	454	22	0.048	160	21
RMNH 588	Java	♂	460	34	0.074	181	20
MHNP 89–193	Borneo	♀	472	22	0.047	179	18
NHMW 16702	Sumatra	♂	490	23	0.047	169	22
margaritophora							
ZSI 14936	Java	♂	200	4	0.020	152	13
MHNP 39186	”	♂	234	8	0.034	150	15
NHMW 16707	”	♂	255	6.5	0.025	157	17
RMNH 4689	Sumatra	♀	256	10	0.039	152	10
RMNH —	”	♀	259	6	0.023	160	11
ZMB 8462	”	♂	261	9	0.034	159	17
USNM 70952	”	♀	358	16	0.045	161	10
bitorques							
MCZ 25776	Phil. Ids.	♀	250	4	0.016	172	15
ZMB 7444	Luzon	♀	329	10	0.030	175	15
ZMB 3778	”	♀	329	16	0.049	157	17
MHNP 00–364	”	♀	328	12	0.037	170	17
CAS 15295	”	♀	398	21	0.053	174	15
SNG 19394	”	♀	412	26	0.063	167	16
MHNP 00–365	”	♀	420	24	0.057	168	15
linnaei							
RMNH —	Java	♀	122	1	0.008	159	9
RMNH —	”	♂	171	2	0.017	140	14
RMNH —	”	♂	233	6	0.026	143	17
RMNH —	”	♀	242	5	0.021	157	8
RMNH —	”	♀	245	6	0.024	154	8
RMNH —	”	♀	281	9	0.032	154	7
RMNH —	”	♀	292	12	0.041	159	8
RMNH —	”	♂	307	20.5	0.067	137	18
RMNH 52	no data	♂	336	20	0.060	150	19
RMNH —	Java	♀	396	38	0.100	154	9
prakkei							
ZSI 13306	Singapore	♂	204	4	0.020	126	32
RMNH 4360	Borneo	♂	243	6.5	0.027	130	31
eiselti							
NHMW 16701:1	Sumatra	♀	244	7	0.029	153	14
NHMW 16703:4	”	♂	333	22	0.066	137	22
NHMW 16703:1	”	♂	343	21	0.061	137	21
NHMW 16703:3	”	♀	365	24	0.066	151	13
CNHM 134723	”	♀	381	28	0.073	151	14
NHMW 16703:2	”	♀	424	42	0.099	151	15

As with many other characters, the many known species of *Calamaria* can be arranged in order of increasing thickness and form a continuous gradient from one extreme to the other.

Coloration.—Taken as a whole, the genus *Calamaria* is highly variable. The dorsal pattern may consist of broad or narrow stripes, narrow or broad transverse bands, and spots of varying sizes. Or the dorsum may be unmarked or divided into dark upper and light lower portions. The individual scales, where they are not involved in the spots, stripes, and bands of the pattern, may be a solid color (e.g., Fig. 40), or have a fine network or speckling on a contrasting background (e.g., Fig. 33). In many species the scales of the first row have light centers and dark edges and form a continuous light stripe or a row of light dots. Dorsally the head usually has the ground color of the body, often with obscure, irregular spots. The upper lip and the underside of the head are usually light and often have dark spots on scale sutures. In a few species the head and trunk colors contrast sharply.

The ventrals of most species are yellow or whitish. The commonest pattern consists of a dark spot at the lateral corners of each ventral. In some species (e.g., *eiselti*) the anterior ventrals are yellow whereas those farther back have a black area that becomes progressively larger on successive plates until it covers the entire width of the belly. In some species each ventral has a dark anterior band and a light posterior one (Fig. 56). A pattern consisting of wider dark bands on a light background occurs in two species. A checkered pattern (Fig. 13) occurs in several species.

The ventral surface of the tail usually has a continuation of the belly coloration, often with the addition of a dark mid-ventral stripe.

Some variation occurs in almost all species. But the type and extent of intraspecific variation differ from species to species. In some species, for example *linnaei*, both dorsal and ventral colorations vary widely (Figs. 12 and 13). Others, e.g., *griswoldi* (Fig. 23) do not vary at all. Although we have seen many more *linnaei* (659) than *griswoldi* (12), the differences between these two species in extent of variation is not attributable to sample size because rarely do any two specimens of *linnaei* resemble one another as much as do all 12 of the *griswoldi*.

The patterns of the different parts of the body may vary in different ways. Generally, the coloration of the head varies less than the trunk. In *alidae* (p. 236), for example, the trunk may be striped, spotted, or banded, whereas the head varies only in the number of dark spots. By contrast, the trunk of *schlegeli* (335 examined) is always dark brown or black above the unspotted, yellow first two scale rows, whereas the head may be completely yellow or completely dark brown or any intermediate bicolored condition.

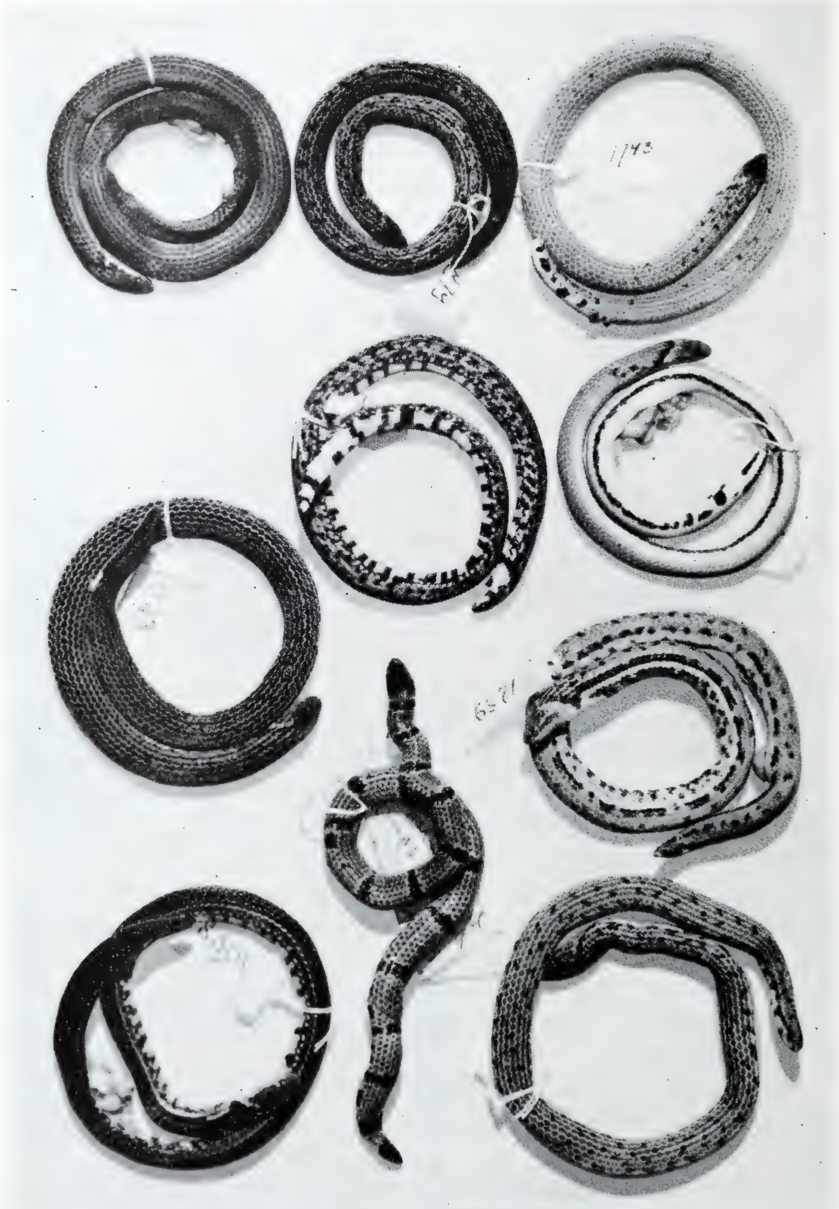

FIG. 12. Individual variation in dorsal pattern of *Calamaria linnaei* from Tjikadjang, Java. Specimen at bottom of middle row from Bandung, Java.

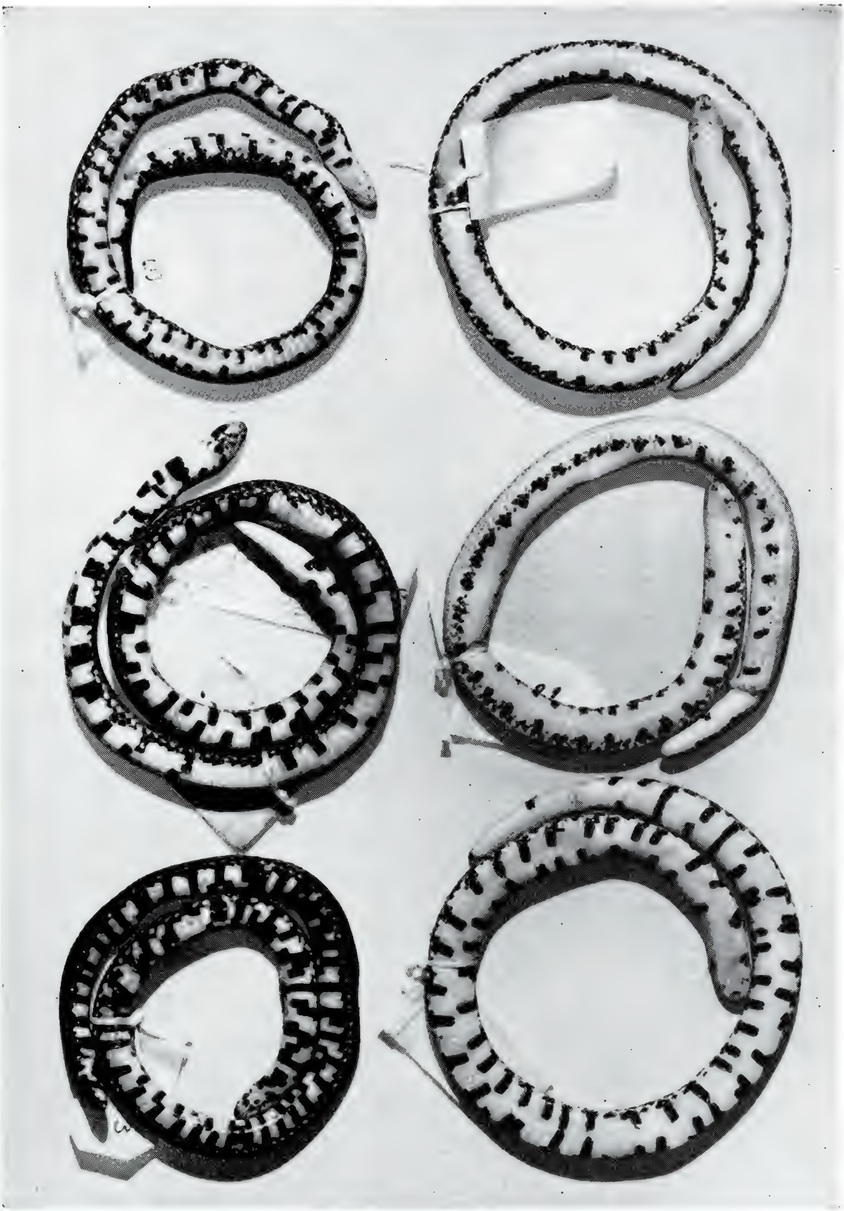

FIG. 13. Individual variation in ventral pattern of *Calamaria linnaei* from Tjikadjang, Java.

Ontogenetic variation characterizes *lumbricoidea* (p. 82) and probably *bicolor* (p. 153). In *lumbricoidea* both head and trunk are involved but though darkening of the color is the age trend, the change is not exactly parallel in the two areas (Figs. 21 and 22). In *bicolor* the entire dorsal surface, except for the tail, becomes darker with age.

Intraspecific variation may be common in a local population. All of the snakes (*linnaei*) in Figs. 12 and 13 except one are from Tjikadjang, Java. At Bukit Tinggi, Sumatra, seven *schlegeli* have three of the types of head coloration listed in Table 44. Other species may show little individual or local but conspicuous geographic variation. All specimens of *lumbricoidea* from Borneo are uniformly dark brown above the first two scale rows; those from the Philippine Islands are striped; those from eastern Sumatra are non-striped and those from western Sumatra striped (Table 21).

Despite local and geographic intraspecific variation, coloration frequently is one of the characters differentiating similar species. Striped *griswoldi*, for example, is immediately distinguishable from the sympatric, non-striped population of *lumbricoidea*. Even striped *lumbricoidea* differ from *griswoldi* as the light lines of the former are confined to the very edges of the mid-dorsal scales whereas in *griswoldi* they cover at least the lateral fourths of each scale (Fig. 23). Furthermore, the belly of *griswoldi* is immaculate yellow and that of *lumbricoidea* is almost always banded. Another example of interspecific variation involves *gervaisi*, which is non-banded, and *bitorques* which is. *Calamaria crassa* and *eiselti* form another closely related pair differing in coloration (cf. Figs. 46 and 47).

Interspecific differences are not universal, however, and some species (e.g., *grabowskyi*, *suluensis*, and *palavanensis*) cannot be distinguished on the basis of coloration. Because of such interspecific similarity and because of wide intraspecific variation in other cases, color differences have to be carefully analyzed in conjunction with other characters before interpretations are made. But this caveat applies to most of the characters used in this study.

Correlation of head characters.—Although a certain amount of individual variation occurs in most characters, we consider a species to be variable (e.g., preocular present or absent; mental touching or not touching chin shields) for the purposes of this section only if the variation is geographic or if, as in the case of *lumholtzi*, the two to four specimens examined were variable.

Association of pairs of cephalic characters was tested by means of contingency tables. Chi-square values reached significant levels

TABLE 14.—Association of Presence of Preocular with Size of Eye in Species of *Calamaria* (Numbers in body of table are numbers of species).

	Preocular						
	Observed				Calculated		
Eye size[1]	Present	Present or absent	Absent	Total	Present	Present or absent	Absent
Greater	16	0	0	16	12.5	0.6	2.8
Equal	19	0	3	22	17.2	0.9	4.0
Less	4	2	6	12	9.4	0.5	2.2

chi-square=20.1; n=4; P <0.001

[1] "Greater," "equal," and "less" refer to eye diameter relative to distance of eye from mouth. Species varying from "less" to "equal" or from "equal" to "greater" are listed as "equal."

($P \leq 0.05$) in only five tests: preocular and eye size (Table 14); frontal ratio and eye size (Table 15); preocular and frontal ratio (Table 16); preocular and relation of mental to chin shields (Table 17); number of scales surrounding paraparietal and number of supralabials (Table 18). Results of tests between all pairs of the cephalic characters are summarized in Table 19.

The association of frontal ratio, eye size, and preocular based earlier on data taken from literature (Marx and Inger, 1955), is confirmed by the material we have since examined (Tables 14–16). These three topographically related characters tend to change as a unit and are what Cain and Harrison (1960) call "necessary corre-

TABLE 15.—Association of Frontal Ratio with Size of Eye in Species of *Calamaria* (Numbers in body of table are numbers of species).

	Eye size						
	Observed				Calculated		
Frontal ratio[1]	Greater	Equal	Less	Total	Greater	Equal	Less
–2	3	0	0	3	1.0	1.3	0.7
2–2⅓	10	5	1	16	5.1	7.0	3.8
2½–$2\frac{4}{5}$	3	5	3	11	3.5	4.8	2.6
3–3½	0	10	4	14	4.5	6.2	3.4
4–	0	2	4	6	1.9	2.6	1.4

Chi-square=27.2; n=8; P <0.001

[1] Ratio of frontal width to supraocular width. Species categorized by intraspecific maxima.

TABLE 16.—Association of Presence of Preocular with Frontal Ratio in Species of *Calamaria* (Numbers in body of table are numbers of species).

Preocular

Frontal ratio	Observed: Present	Observed: Present or absent	Observed: Absent	Total	Calculated: Present	Calculated: Present or absent	Calculated: Absent
–2	3	0	0	3	2.4	0.1	0.5
2–2⅓	16	0	0	16	12.5	0.6	2.9
2½–2⅘	9	1	1	11	8.6	0.4	2.0
3–3½	9	0	5	14	10.9	0.6	2.5
4–	2	1	3	6	4.7	0.2	1.1
Total	39	2	9		39.1	1.9	9.0

Chi-square=18.2; n=8; P=0.05

lates." Their association prohibits the use of them as three independent estimates of similarity or divergence. Yet it would be an oversimplification to say that we are dealing with a single character, the ocular region, in taxonomic evaluation of a comparison. For as the association is not perfect, the parts of this unit have changed at different rates. A small ocular region may be one in which the preocular has disappeared while the eye has remained moderate in size (e.g., *javanica*), one in which the eye has become small while the preocular has not disappeared (e.g., *hilleniusi*), or one in which both eye and preocular have become reduced (e.g., *schlegeli cuvieri*). Thus despite their association, each of these characters has to be considered in evaluating a comparison of two samples.

TABLE 17.—Association of Presence of Preocular with Relation of Mental to Chin Shields in Species of *Calamaria*
(Numbers in body of table are numbers of species).

Preocular

Mental and chin shield	Observed: Present	Observed: Present or absent	Observed: Absent	Total	Calculated: Present	Calculated: Present or absent	Calculated: Absent
Separated	12	2	5	19	14.8	0.8	3.4
Separated or touching	2	0	2	4	3.1	0.1	0.7
Touching	25	0	2	27	21.1	1.1	4.9

Chi-square=9.5; n=4; P=0.05

TABLE 18.—Association of Number of Scales Surrounding Paraparietal with Number of Supralabials in Species of *Calamaria*.

(Numbers in body of table are numbers of species)

Scales surrounding paraparietal

Supra-labials	Observed			Total	Calculated		
	5	*5* or *6*	*6*		*5*	*5* or *6*	*6*
4	1	0	10	11	5.1	0.4	5.5
5	22	2	15	39	17.9	1.6	19.5

Chi-square=9.4; n=2; P=0.01

The association of number of scales surrounding the paraparietal with number of supralabials does not have an obvious explanation. The reduction from five to four supralabials occurs in the preorbital region (Marx and Inger, 1955, p. 169) and has no apparent functional relation to an increase in number of scales at the rear of the head. Correlations of this sort, which does not involve necessary correlates, are valuable in attempts to evaluate the relations of populations as they provide additional evidence of common genotypes.

Association of the preocular character with the relation between mental and chin shields has no obvious explanation. Separation of mental and chin shields occurs proportionately oftener with the absence of a preocular than one would expect on the basis of chance alone. Contact between mental and chin shields is probably the primitive condition in this genus (p. 254) and absence of preocular advanced (p. 254). Thus the association shown in Table 17 does not result from progressive modification of both characters. Loss of the

TABLE 19.—Summary of Chi-Square Tests of Association Between Pairs of Cephalic Characters in Species of *Calamaria*.

(Value of chi-square in upper right half of table, with degrees of freedom as superscripts. Corresponding values of P in lower left hand. Character states as in Tables 14–18)

	Supra-labials	Preocular	Frontal	Eye size	Mental	Para-parietal
Supralabials	. .	3.5^2	5.1^4	3.9^2	2.1^2	9.4^2
Preoculars	>0.1	. .	18.2^8	20.1^4	9.5^4	5.6^4
Frontal	>0.2	0.05	. .	27.2^8	13.0^8	13.9^8
Eye size	>0.1	<0.001	<0.001	. .	5.9^4	2.6^4
Mental	>0.3	0.05	>0.1	0.2	. .	6.6^4
Paraparietal	0.01	>0.2	0.09	>0.5	>0.1	. .

preocular is correlated with general reduction in the ocular region. The other characters associated with the preocular reduction of the ocular region, namely eye size and frontal ratio, are not associated with the chin character (Table 19). Consequently the association of preocular and mental appears not to have a functional basis. As these characters are not necessary correlates, both may be used as independent estimates of similarity or divergence of populations.

KEY TO FORMS OF *CALAMARIA*

1. One supralabial entering orbit . . . . . . *lowi lowi* (p. 222)
Two supralabials entering orbit 2

2. Second and third supralabials entering orbit 3
Third and fourth supralabials entering orbit 16

3. Preocular absent 4
Preocular present 9

4. Mental not touching anterior chin shields 5
Mental touching anterior chin shields 7

5. Supraocular and postocular fused into a single shield . . . . . . *gracillima* (p. 229)
Supraocular distinct from postocular 6

6. Frontal 5 to 6 times width of supraocular; nasal larger than postocular; maxillary teeth unmodified (fig. 2 top) . . . . . . *schmidti* (p. 74)
Frontal 2⅓ to 4 times width of supraocular; nasal equal to, or smaller than postocular; maxillary teeth modified (fig. 2 bottom) . . . *lowi gimletti* (p. 226)

7. Eye much smaller than eye-mouth distance; posterior chin shields meeting in midline 8
Eye equal to eye-mouth distance; posterior chin shields not meeting in midline . . . . . . *javanica* (p. 209)

8. Posterior ventrals dark brown . . . . . . *lowi lowi* (p. 222)
Posterior ventrals cream colored . . . . . . *lowi wermuthi* (p. 225)

9. Two infralabials touching anterior chin shields . . . . . . *borneensis* (p. 194)
Three infralabials touching anterior chin shields 10

10. Mental touching anterior chin shields 11
Mental not touching anterior chin shields 15

11. Each ventral with a dark anterior half and a light posterior half 12
Ventrals never transversely divided into light and dark halves 13

12. Narrow longitudinal stripes mid-dorsally; tail tapering abruptly at end. *battersbyi* (p. 208)
No longitudinal stripes mid-dorsally; tail tapering in posterior half. *melanota* (p. 198)

13. Length of parietal greater than distance from rostral to posterior tip of frontal. *buchi* (p. 211)
Length of parietal less than distance from rostral to posterior tip of frontal . . 14

14. Ventrals with black rectangular markings; or if not, lateral corners of successive ventrals not identical in color (fig. 13) . . . . . . *linnaei* (p. 200)
Lateral corners of every ventral identical, dark; dark mid-ventral pigment, if present, confined to a very few dots irregularly scattered. *pavimentata* (p. 212)

15. Tail as thick as body, not tapering, blunt (fig. 10A)...*septentrionalis* (p. 218)
Tail not as thick as body, tapered, pointed............*pavimentata* (p. 212)

16. Preocular absent..17
Preocular present..23

17. A continuous dark mid-dorsal stripe occupying scales in vertebral row.
mecheli (p. 233)
Without continuous dark vertebral stripe..............................18

18. Each ventral with a dark anterior half and a light posterior half or completely dark..*apraeocularis* (p. 237)
Ventrals cream-colored centrally or with a few irregularly scattered dark spots..19

19. A light longitudinal stripe on second and third scale rows, bordered below by a dark stripe on first row..............................*lumholtzi* (p. 148)
Stripes, if present, not as above..............................20

20. Tail thick, not tapered, end broadly rounded (fig. 14A).......*alidae* (p. 235)
Tail tapered at least in posterior fourth (fig. 14B)......................21

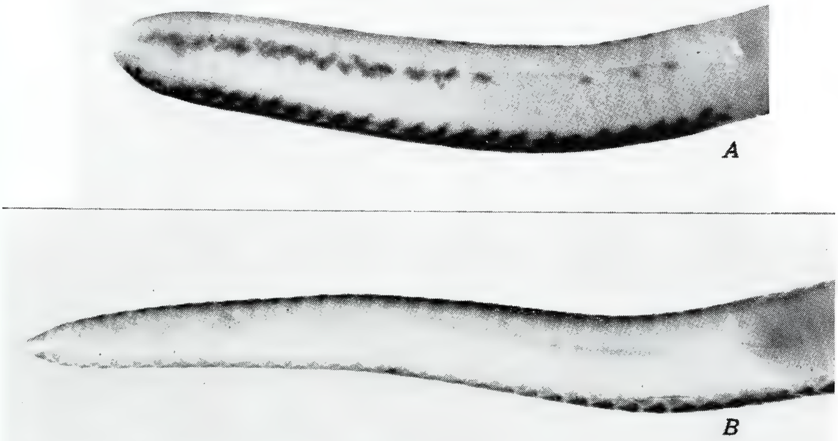

FIG. 14 Ventral views of tails in males of *Calamaria alidae* (A) and *C. schlegeli* (B).

21. Most of dorsal scales dark brown with a light network, or yellowish with a dark network (as in fig. 33)..............................22
Each dorsal scale above the second row dark brown without a light network (fig. 43)..*schlegeli* (p. 154)

22. A narrow, light nuchal collar..........................*ceramensis* (p. 232)
No nuchal collar..*rebentischi* (p. 230)

23. Mental not touching anterior chin shields..............................24
Mental touching anterior chin shields..............................42

24. Maxillary teeth unmodified (fig. 2 top)..............................25
Maxillary teeth modified (fig. 2 bottom)..............................27

25. Six shields and scales surrounding paraparietal (as in fig. 1 bottom). *lautensis* (p. 70)
Five shields and scales surrounding paraparietal (as in fig. 1 top)........26

26. No dark pigment on ventrals........................*leucogaster* (p. 63)
Dark pigment on outer edges of ventrals..................*ulmeri* (p. 68)

27. Dorsum with wide, dark, transverse crossbands four or more dorsal scales wide. *bicolor* (p. 149)
Dorsum lacking crossbands, or if present, one or two scale rows wide......28

28. Ventral coloration as dark as dorsal, the two areas separated by a white stripe. *lateralis* (p. 146)
Coloration of dorsum different from that of ventrum..................29

29. A single, light continuous stripe on second and third scale rows. *lumholtzi* (p. 148)
If stripe is present, not occupying above position on lateral scale rows....30

30. Five scales and shields surrounding paraparietal (as in fig. 1 top)........31
Six scales and shields surrounding paraparietal (as in fig. 1 bottom)......37

31. All ventrals behind first fourth of body with dark pigmentation at least on their lateral tips..33
Almost all ventrals without pigmentation..........................32

32. Prefrontal not touching third supralabial................*schlegeli* (p. 154)
Prefrontal touching third supralabial......................*bicolor* (p. 149)

33. Reduction to four dorsal scale rows on tail more than 13 subcaudals from tip. *everetti* (p. 133)
Reduction to four dorsal scale rows on tail 13 or fewer subcaudals from tip..34

34. Oblique black stripe running from eye to corner of mouth.*brongersmai* (p. 118)
No oblique black stripe running back of eye..........................35

35. Diameter of eye longer than ventral border of prefrontal.*palavanensis* (p. 134)
Diameter of eye not longer than ventral border of prefrontal............36

36. Tail blunt (fig. 15A)....................................*virgulata* (p. 186)
Tail tapering to a point (fig. 15B)........................*modesta* (p. 138)

37. Dorsum with narrow dark crossbands...............................38
Dorsum without narrow dark crossbands.............................39

38. Eye less than eye-mouth distance.....................*döderleini* (p. 177)
Eye 1½ times eye-mouth distance.....................*boesemani* (p. 171)

39. Eye 1½ times eye-mouth distance.....................*boesemani* (p. 171)
Eye, at its largest, slightly greater than eye-mouth distance............40

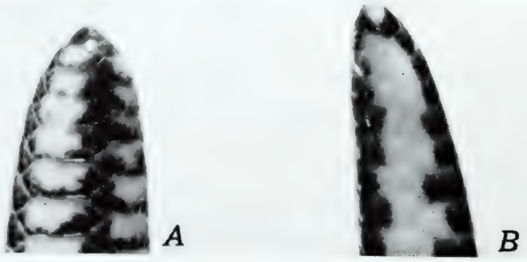

FIG. 15. Ends of tails of *Calamaria virgulata* (A) and *C. modesta* (B).

40. Tail ending bluntly (fig. 15A)........*virgulata* (p. 186)
Tail tapering to a point (figs. 14B, 15B)........41

41. Ventrals with dark pigment at least at lateral tips........*modesta* (p. 138)
Ventrals without dark pigment........*schlegeli* (p. 154)

42. Maxillary teeth unmodified (fig. 2 top)........43
Maxillary teeth modified (fig. 2 bottom)........44

43. Posterior chin shields meeting in midline........*curta* (p. 71)
Posterior chin shields not meeting in midline........*acutirostris* (p. 73)

44. Paraparietal surrounded by 6 shields and scales (as in fig. 1 bottom)........45
Paraparietal surrounded by 5 shields and scales (as in fig. 1 top)........53

45. Ventrals 176 or more........46
Ventrals 175 or less........47

46. No dark transverse bands behind head........*virgulata* (p. 186)
At least 2 transverse bands behind head........*forcarti* (p. 184)

47. Dark pigment of ventrals restricted to lateral corners........48
Ventrals in posterior half of body with dark pigment across entire width........51

48. A continuous dark vertebral stripe formed by spots on each vertebral scale (fig. 51)........*sumatrana* (p. 181)
If vertebral spots present, not forming continuous stripe for entire length of body........49

49. Subcaudals of males 24 or more, of females 14........*abstrusa* (p. 179)
Subcaudals of males 20 or less, of females 11 or less........50

50. Dark spots on dorsal scales forming short lines 2 to 5 scales long (fig. 44); frontal shorter than parietal........*margaritophora* (p. 166)
Dark spots on dorsal scales not forming lines; frontal equal to or longer than parietal........*nuchalis* (p. 170)

51. Underside of tail with dark crossbands more than one subcaudal wide.
eiselti (p. 175)
Underside of tail without crossbands, or if present, less than one subcaudal wide........52

52. Sides of neck with triangular extensions of light ventral coloration; diameter of eye greater than eye-mouth distance........*crassa* (p. 173)
Sides of neck without triangular extensions of ventral coloration; diameter of eye equal to or smaller than eye-mouth distance........*virgulata* (p. 186)

53. Two light stripes on each side of body (fig. 24)........*albiventer* (p. 94)
Not colored as above........54

54. Four or five light stripes running length of body on each side (fig. 23)........55
No light stripes above first scale row........56

55. Belly immaculate yellow........*griswoldi* (p. 92)
Belly with dark crossbands or almost completely black........*lumbricoidea* (p. 75)

56. Dorsal scales above third row solid dark color without network (fig. 25)........57
Most of dorsal scales above third row dark with light network or light with dark network (fig. 33)........58

57. Eye small, its diameter about two-thirds eye-mouth distance (fig. 25).
hilleniusi (p. 96)
Eye larger, at its smallest slightly less than eye-mouth distance.
lumbricoidea (p. 75)

58. Two to six dark, black-edged, wide crossbands behind head (fig. 27).
bitorques (p. 104)
No such crossbands........59

59. Scales of first row with yellow or white centers forming a stripe or row of light dots running length of body 60
No row of light dots or light stripe on first scale row 64

60. A continuous or narrowly interrupted light nuchal collar 61
No light nuchal collar 62

61. Subcaudals in males more than 30, in females more than 20 . . *prakkei* (p. 120)
Subcaudals in males less than 25, in females less than 20 . . . . . *gervaisi* (p. 106)

62. Light centers of scales in first row forming row of light dots . . . *gervaisi* (p. 106)
Light centers of scales in first row forming uninterrupted stripe 63

63. Ventrals in males 150 or more, in females usually more than 164. *grabowskyi* (p. 00)
Ventrals in males less than 140, in females usually less than 164. *suluensis* (p. 123)

64. Eye small, its diameter about two-thirds eye-mouth distance. *joloensis* (p. 102)
Eye larger, at its smallest slightly less than eye-mouth distance 65

65. Head pointed, distinctly tapered in front of eye (fig. 26) . . . . . *muelleri* (p. 99)
Head rounded, not conspicuously tapered in front of eyes (fig. 28). *gervaisi* (p. 106)

KEY TO SPECIES OF *CALAMARIA* FROM BORNEO

1. Third or second and third supralabials entering orbit 2
Third and fourth supralabials entering orbit 7

2. Preocular absent 3
Preocular present 5

3. Supraocular and postocular fused into a single shield . . . . . *gracillima* (p. 229)
Supraocular distinct from postocular 4

4. Mental touching anterior chin shields . . . . *lowi* (p. 221)
Mental not touching anterior chin shields . . . . *schmidti* (p. 74)

5. Two infralabials touching anterior chin shield . . . . *borneensis* (p. 194)
Three infralabials touching anterior chin shield 6

6. Narrow longitudinal stripes mid-dorsally; tail short, tapering abruptly at end. *battersbyi* (p. 208)
No longitudinal stripes mid-dorsally; tail longer, tapering in posterior half. *melanota* (p. 198)

7. A light longitudinal stripe on second and third scale rows bordered below by a dark stripe on first row . . . . *lumholtzi* (p. 148)
Stripes, if present, not as above 8

8. Preocular absent 9
Preocular present 10

9. Most of dorsal scales dark brown with a light network or yellowish with a dark network . . . . *rebentischi* (p. 230)
Each dorsal scale above the second row dark brown without a light network. *schlegeli* (p. 154)

10. Mental not touching the anterior chin shields 11
Mental touching anterior chin shields 18

11. Dorsum with wide dark transverse crossbands four or more scale rows wide. *bicolor* (p. 149)
Dorsum lacking crossbands 12

12. Ventral and dorsal coloration dark brown with a bold continuous lateral white stripe . . . . *lateralis* (p. 146)
Ventral coloration different from dorsal coloration 13

13. Almost all ventrals without dark pigmentation 14
All ventrals behind first fourth of body with dark pigmentation at least on their lateral tips 16

14. Eye larger than eye-mouth distance . . . . *leucogaster* (p. 63)
Eye smaller than eye-mouth distance 15

15. Prefrontal not touching third supralabial . . . . *schlegeli* (p. 154)
Prefrontal usually touching third supralabial . . . . *bicolor* (p. 149)

16. Reduction to four dorsal scale rows on tail 14 or more subcaudals from tip. *everetti* (p. 133)
Reduction to four dorsal scale rows on tail 13 or fewer subcaudals from tip . . 17

17. Tail ending in a blunt tip (fig. 15A) . . . . *virgulata* (p. 186)
Tail tapering to a point . . . . *modesta* (p. 138)

18. Belly with dark crossbands, each more than one ventral wide. *lumbricoidea* (p. 75)
Belly not cross-banded or with bands narrower than one ventral 19

19. Eye two-thirds eye-mouth distance . . . . *hilleniusi* (p. 96)
Eye equal to or greater than eye-mouth distance 20

20. Dorsum with longitudinal dark and light stripes . . . . *griswoldi* (p. 92)
Mid-dorsal region not striped 21

21. Tail thick, tapering abruptly near end to a blunt tip . . . . *prakkei* (p. 120)
Tail tapering gradually 22

22. Ventrals of males under 145, of females usually less than 164 . *suluensis* (p. 123)
Ventrals of males 145 or more, of females usually more than 164. *grabowskyi* (p. 129)

KEY TO SPECIES OF *CALAMARIA* FROM SUMATRA

1. Preocular absent 2
Preocular present 4

2. Dark stripe on vertebral row . . . . *mecheli* (p. 233)
Without dark stripe on vertebral row 3

3. Ventrals 185 or more . . . . *alidae* (p. 235)
Ventrals 159 or less . . . . *schlegeli* (p. 154)

4. Mental not touching anterior chin shields 5
Mental touching anterior chin shields 10

5. Dorsum with narrow dark crossbands . . . . *döderleini* (p. 177)
Dorsum without crossbands 6

6. Ventrals without dark pigment on lateral edges 7
Ventrals with dark pigment at least on lateral edges 8

7. Eye smaller than eye-mouth distance . . . . *schlegeli* (p. 154)
Eye greater than eye-mouth distance . . . . *leucogaster* (p. 63)

8. Unmodified maxillary teeth (fig. 2 top) . . . . *ulmeri* (p. 68)
Modified maxillary teeth (fig. 2 bottom) 9

9. Tail thick and blunt (fig. 15A) . . . . *virgulata* (p. 186)
Tail tapering to a point (fig. 15B) . . . . *modesta* (p. 138)

10. Paraparietal surrounded by 6 scales and shields (as in fig. 1 bottom) 11
Paraparietal surrounded by 5 scales and shields (as in fig. 1 top) 16

11. Ventrals 176 or more . . . . *forcarti* (p. 184)
Ventals 175 or less 12

12. Ventrals in posterior half of body with dark pigment across entire width 13
Ventrals at most with dark pigment restricted to lateral corners 14

13. Underside of tail cross-banded . . . . *eiselti* (p. 175)
Underside of tail not cross-banded . . . . *crassa* (p. 173)

14. A continuous dark vertebral stripe formed by spots on each vertebral scale. *sumatrana* (p. 181)
If vertebral stripe present, interrupted 15

15. Subcaudals of males 24 or more, of females 14 . . . . *abstrusa* (p. 179)
Subcaudals of males 17 or fewer, of females 11 or fewer . *margaritophora* (p. 166)

16. Two pairs of light stripes . . . . *albiventer* (p. 94)
No stripes, or more than two pairs of light stripes . . . . *lumbricoidea* (p. 75)

KEY TO SPECIES OF *CALAMARIA* FROM ASIATIC MAINLAND

1. Third and fourth supralabials enter orbit 2
Second and third supralabials enter orbit 5

2. Mental not touching anterior chin shields . . . . *schlegeli* (p. 154)
Mental touching anterior chin shields 3

3. Belly with dark crossbands . . . . *lumbricoidea* (p. 75)
Belly without crossbands 4

4. Light dorsolateral stripe present (fig. 24) . . . . *albiventer* (p. 94)
No light dorsolateral stripe . . . . *prakkei* (p. 120)

5. Preocular absent . . . . *lowi* (p. 221)
Preocular present 6

6. Ventrals yellow, immaculate . . . . *buchi* (p. 211)
Ventrals yellow, with dark lateral tips 7

7. Tail as thick as body, not tapering, end broadly rounded (fig. 10A). *septentrionalis* (p. 218)
Tail not thick as body, tapered, pointed . . . . *pavimentata* (p. 212)

KEY TO SPECIES OF *CALAMARIA* FROM JAVA

1. Second and third supralabials entering orbit 2
Third and fourth supralabials entering orbit 4

2. Preocular present . . . . *linnaei* (p. 200)
Preocular absent 3

3. Posterior chin shields meet in midline . . . . *lowi wermuthi* (p. 225)
Posterior chin shields do not meet in midline . . . . *javanica* (p. 209)

4. Mental not touching anterior chin shields 5
Mental touching anterior chin shields . . . . *lumbricoidea* (p. 75)

5. Preocular absent . . . . *schlegeli* (p. 154)
Preocular present 6

6. Five scales and shields surrounding paraparietal (as in fig. 1 top) 7
Six scales and shields surrounding paraparietal (as in fig. 1 bottom) 9

7. Ventral coloration as dark as dorsal, the two areas separated by a white stripe. *lateralis* (p. 146)
Ventral coloration different from dorsal coloration 8

8. Eye greater than eye-mouth distance .... *leucogaster* (p. 63)
Eye less than eye-mouth distance .... *bicolor* (p. 149)

9. Tail thick and blunt (fig. 15A) .... *virgulata* (p. 186)
Tail tapering to a point (fig. 15B) .... *modesta* (p. 138)

KEY TO SPECIES OF *CALAMARIA* FROM CELEBES AND MOLUCCAS

1. Preocular absent 9
Preocular present 2

2. Mental not touching anterior chin shields 3
Mental touching anterior chin shields 5

3. Paraparietal surrounded by six scales and shields (as in fig. 1 bottom) 4
Paraparietal surrounded by five scales and shields (as in fig. 1 top). *brongersmai* (p. 118)

4. Eye almost 1½ times eye-mouth distance .... *boesemani* (p. 171)
Eye, at its largest, slightly greater than eye-mouth distance . *virgulata* (p. 186)

5. First gular touching anterior chin shields .... *acutirostris* (p. 73)
First gular not touching anterior chin shields 6

6. Paraparietal surrounded by six scales and shields (as in fig. 1 bottom) 7
Paraparietal surrounded by five scales and shields (as in fig. 1 top). *muelleri* (p. 99)

7. Tail thick, tapering abruptly at end (fig. 15A) .... *virgulata* (p. 186)
Tail tapering gradually from base 8

8. Ventrals yellow, immaculate except for dark lateral tips .... *nuchalis* (p. 170)
Ventrals dark, yellowish on posterior edges only .... *curta* (p. 71)

9. Mental touching anterior chin shields .... *apraeocularis* (p. 237)
Mental not touching anterior chin shields .... *ceramensis* (p. 232)

KEY TO SPECIES OF *CALAMARIA* FROM PHILIPPINE ISLANDS

1. Mental not touching anterior chin shields 2
Mental touching anterior chin shields 3

2. Subcaudals of males 21 or less, of females 14 or less .... *virgulata* (p. 186)
Subcaudals of males 23 or more, of females 16 or more .... *palavanensis* (p. 134)

3. Belly with dark crossbands .... *lumbricoidea* (p. 75)
Belly without crossbands 4

4. Two to six dark, black-edged crossbands behind head (fig. 27). *bitorques* (p. 104)
No black-edged, dark crossbands behind head 5

5. Eye smaller than eye-mouth distance .... *joloensis* (p. 102)
Eye equal to or greater than eye-mouth distance .... *gervaisi* (p. 106)

SPECIES ACCOUNTS

Calamaria leucogaster Bleeker. Figure 16.

Calamaria leucogaster Bleeker, 1860, Nat. Tijds. Ned. Indie., **21**, p. 293—Ampat Lawang, Sumatra; Günther, 1865, Ann. Mag. Nat. Hist., (3), **15**, p. 89; Edeling, 1870, Nat. Tijds. Ned. Indie, **31**, p. 381; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 341; Bartlett, 1895, Sarawak Note Book, no. 1, p. 84; Baumann, 1913, Zool. Jahrb., (Syst.), **34**, p. 271; Mertens, 1924, Zool. Anz., **60**, p. 159; Jong, 1928, Treubia, **10**, p. 147; Werner, 1929, Zool. Jahrb., (Syst), **57**, p. 172; Angel, 1941, Bull. Mus. Nat. Hist. Nat., (2), **13**, p. 412; de Haas, 1950, Treubia, **20**, p. 569; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 179.

Calamaria arcticeps Günther, 1866, Ann. Mag. Nat. Hist., (3), **18**, p. 25, pl. 4, fig. C—Borneo; Mocquard, 1890, Nouv. Arch. Mus. Paris, (3), **2**, p. 120.

Calamaria beccari Peters, 1872, Ann. Mus. Genova, **3**, p. 34—Sarawak; Mocquard, 1890, *loc. cit.*, p. 120; Boulenger, 1894, *op. cit.*, p. 343; Werner, 1929, *loc. cit.*, p. 172; de Haas, 1950, *loc. cit.*, p. 564; Marx and Inger, 1955, *loc. cit.*, p. 200.

Calamaria brookii Boulenger, 1895, Ann. Mag. Nat. Hist., (6), **15**, p. 329—Matang, Sarawak; Boulenger, 1894, *op. cit.*, **3**, p. 647; Bartlett, 1895, *op. cit.*, p. 85; 1896, *ibid.*, no. 2, p. 116; Werner, 1929, *loc. cit.*, p. 172; de Haas, 1950, *loc. cit.*, p. 565.

Calamaria smithi Dunn, 1923, Jour. Malayan Asiat. Soc., **1**, p. 3—Long Mujan, Sarawak; Werner, 1929, *loc. cit.*, p. 172; de Haas, 1950, *loc. cit.*, p. 574; Marx and Inger, 1955, *loc. cit.*, p. 206.

Calamaria leucocephala (non Duméril and Bibron), Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., p. 84.

Calamaria bicolor (non Duméril and Bibron), Vogt, 1925, Zool. Anz., **62**, p. 64.

Syntypes.—British Museum (Natural History) 63.12.11.141; Rijksmuseum van Natuurlijke Historie 3994.

Taxonomic notes.—The holotypes of *arcticeps, beccari, brookii,* and *smithi* are identical to the syntypes of *leucogaster* except that the last are unstriped.

Günther's description (1866) did not mention the oculars of *articeps.* However, Mr. J. C. Battersby has kindly examined the holotype at our request and informs us that a preocular is present.

Peters (1872) was in error in reporting that the holotype of *beccari* had 2 postoculars. It is a typical Bornean *leucogaster* with a single postocular.

Diagnosis.—Maxillary teeth unmodified (Fig. 2, top); third and fourth supralabials enter orbit; mental not touching anterior chin shields; paraparietal surrounded by 5 shields and scales; no dark pigment on ventrals.

Description.—Rostral usually higher than wide, portion visible from above less than ½ length of prefrontal suture; prefrontal subequal to frontal, touching first 2 supralabials; frontal hexagonal, 1¾ to 4½ times width of supraocular, about ¾ length of parietal; parietal 1⅓ times length of prefrontal; paraparietal usually (19 of 23) surrounded by 5 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, second next largest, other 3 subequal; mental triangular, separated from anterior chin shields in all but 2 specimens; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.006–0.028 (7 specimens); tail tapering near tip to a sharp point; dorsal scales reduce to 4 rows on tail opposite third to sixteenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth subcaudal, retractor muscle beginning opposite tenth subcaudal, sulcus bifurcate, calyces smooth (2 specimens). Cloaca of female bilobed (2 specimens).

Seven to 8 unmodified maxillary teeth (8 specimens).

Ventrals: males, 126–146 (mean 125.4; N=12); females, 129–157 (mean 145.6; N=21). Subcaudals: males, 17–26 (mean 21.2; N=14); females, 12–19 (mean 15.4; N=22).

Total length: males, 75–219 mm.; females, 82–223 mm. Ratio of tail to total length: males, 0.085–0.135 (mean 0.106; N=12); females, 0.056–0.092 (mean 0.071; N=18).

Ground color dark brown, dorsal scales usually with a light or dark network; body with or without dark longitudinal stripes; the striped pattern consisting of a narrow dark stripe along the edges of the vertebral and paravertebral scale rows, a wider stripe on adjacent halves of the fourth and fifth scale rows, a stripe along adjacent halves of the second and third scale rows, and a thin dark line along the upper edge of the first scale row; lower two-thirds of the first scale

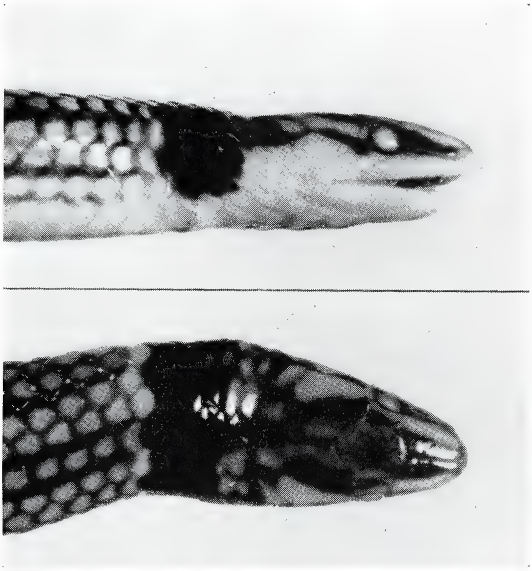

FIG. 16. *Calamaria leucogaster* (CNHM 67279).

row cream-colored; a black collar 2 to 5 scales wide, separated from parietals by 1 to 3 scales and sometimes bordered posteriorly by a narrow yellow ring; a dark ring around body at root of tail, usually a second black ring near tip; head dark brown middorsally with a light streak running through the center of the prefrontal, the lateral edge of the supraocular, and the lateral portion of the parietal; a dark longitudinal stripe along adjacent portions of prefrontals and supralabials, continuing behind eye along adjacent edges of parietal and supralabial; remainder of upper lip and underside of head cream-colored; ventrals and subcaudals cream-colored; tail with a mid-ventral dark stripe in some individuals.

Individual variation.—Only one specimen (SNG 19410) has a dark ventral surface. One (RMNH unnumbered, from Upper Mahakam) has the lateral edges of the ventrals dark.

Two specimens (CNHM 67279, MCZ 43576) have the mental meeting the anterior chin shields at a point. The snake from Upper Mahakam has the mental in broad contact with the anterior chin shields.

One specimen (MHNP 39-188) has the preocular and prefrontal fused on the left side.

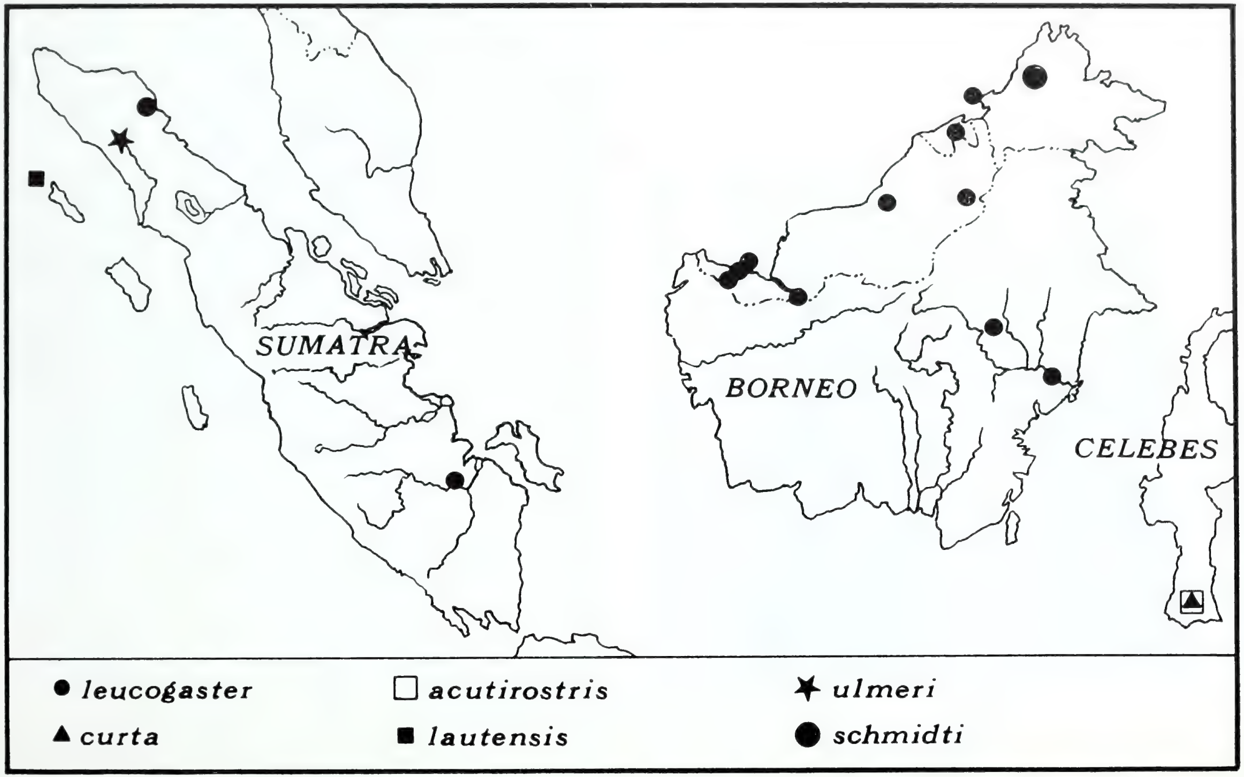

FIG. 17. Distribution of species of *Calamaria* having unmodified maxillary teeth.

TABLE 20.—Geographic Variation in *Calamaria leucogaster*.

Region	No.	Ventrals		Subcaudals		Tail ratio[1]		Reduction[2]	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean
MALES									
Sumatra............	3	126–31	128.0	17–26	20.3	85–135	104	5–9	6.7
Borneo.............	9	127–46	137.4	21–24	22.4	100–124	111	4–16	8.3
FEMALES									
Sumatra............	5	129–46	137.8	12–16	13.6	56–92	66	3–6	4.8
Borneo.............	17	130–57	148.1	14–19	15.9	56–91	71	5–16	6.7

[1] Ratio in thousandths of total length.

[2] Position of reduction to four dorsal scale rows in terms of subcaudals from terminal scute.

Geographic variation.—The striped pattern (Fig. 16) is characteristic of most of the specimens from Borneo, although in 3 the stripes are faint and in 4 they are absent. All Sumatran specimens are unstriped. The 2 presumed to be from Java (see below) have faint stripes. No other geographic variation (Table 20) was found.

Distribution.—Sumatra and Borneo (Fig. 17).

The only specimens reported from Java (MHNP 39–188 and 39–189) were obtained by Boudart. Other specimens Boudart reportedly obtained at Batavia (see p. 170) probably were not collected there. This, in turn, casts doubt on the authenticity of the Javanese locality for *leucogaster.*

SUMATRA (RMNH 3 unnumbered; ZMB 6293, 31403, 33610). Sumatera Utara: Deli (SNG 19410; ZMA 10077). Sumatera Selatan: Ampat Lawang (BM 63.12.11.141-syntype; RMNH 3994-syntype).

SARAWAK (BM 1908.5.28.69; MCG 30456-holotype of *beccari*). Kindi District (BM 1911.1.30.25). First Division: Matang (BM 95.2.28.30-holotype of *brookii;* SM unnumbered), Kuching (SM unnumbered), Santubong (CNHM 71598–99), Bidi, near Bau (SM unnumbered). Second Division: Lubok Antu (SM unnumbered). Third Division: Long Mujan (BM 1922.11.24.5-holotype of *smithi*). Fourth Division: Niah (CNHM 129004, 131601–04). Fifth Division: Lawas (CNHM 67279).

NORTH BORNEO. Kota Belud District: Kiau, 915 meters (NMS 320), Mount Kina Balu (BM 94.6.30.53; MCZ 43575–76). Labuan District: Labuan (BM 94.6.30.52).

INDONESIAN BORNEO: Long Petah (ZMA 10110); Upper Mahakam (RMNH unnumbered).

BORNEO (BM 68.1.27.22; SM 3 unnumbered; ZMB 8012); central Borneo (SMNS 4585).

? Java. Jakarta (MNHP 39–188, 39–189).

Specimens examined.—42.

Calamaria ulmeri Sackett. Figure 18.

Calamaria ulmeri Sackett, 1940, Not. Nat., no. 41, p. 2—northwest of Blangkedjeren, Atjeh Province, Sumatra; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 206.

Holotype.—Academy of Natural Sciences of Philadelphia 21535.

Diagnosis.—Maxillary teeth unmodified; third and fourth supralabials entering orbit; mental not touching anterior chin shields; paraparietal surrounded by 5 shields and scales; lateral corners of ventrals with dark pigment.

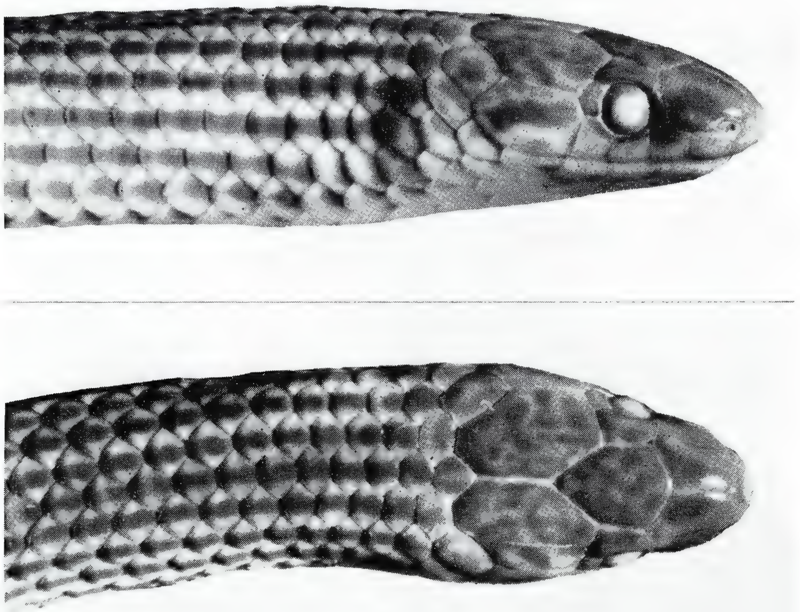

FIG. 18. Holotype of *Calamaria ulmeri.*

Description.—Rostral wider than high, portion visible from above ⅔ length of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 2⅓ times width of supraocular, about ¾ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye twice the eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 3 subequal and slightly larger than fourth; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Tail incomplete but tapering gradually from base; reduction to 4 dorsal scale rows, if it occurs at all, must take place near the end of the tail. Six scale rows are present opposite the twenty-third subcaudal of this incomplete tail.

Ten unmodified maxillary teeth (1 specimen).

Ventrals 186 in female; subcaudals 23+ in female. Snout-vent length, 284 mm.; incomplete tail, 23 mm.

Body and tail brownish above, each scale with a dark network and a dark central spot; these spots unite to form dark stripes running the length of body and tail; head brown above with small dark spots; upper halves of supralabials dark, lower halves yellowish with dark sutures; underside of head yellowish with small dark spots; lateral corners of ventrals and subcaudals dark brown, otherwise entire ventral surface immaculate yellow.

Distribution.—Northern Sumatra (Fig. 17).

SUMATRA. Sumatera Utara: Atjeh Province, about 40 km. northwest of Blangkedjeren, 2080 meters altitude (ANSP 21535-holotype).

Calamaria lautensis de Rooij

Calamaria lautensis (part) de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 163, fig. 66—Pulau Si Laut, Cocos Islands; Werner, 1929, Zool. Jahrb., (Syst)., **57**, p. 172; de Haas, 1950, Treubia, **20**, p. 569; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 203.

Lectotype.—Rijksmuseum van Natuurlijke Historie 4716A, here designated.

Taxonomic notes.—As the Amsterdam Museum syntype (ZMA 10111) from Cocos Islands is damaged, we are selecting one of the Rijksmuseum syntypes as the lectotype. See page 139.

Diagnosis.—Maxillary teeth unmodified; third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; paraparietal surrounded by 6 shields and scales.

Description.—Rostral slightly wider than high, portion visible from above ½ length of prefrontal suture; prefrontal slightly shorter than frontal, touching first 2 supralabials; frontal hexagonal, 2⅓ to 2½ times width of supraocular, about $^3/_5$ length of parietal; parietal 1½ to 1⅔ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye less than eye-mouth distance;

5 supralabials, third and fourth entering orbit, fifth the largest, first, third, and fourth subequal, second slightly larger; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.028 (1 specimen); tail thick, tapering near end to a sharp point; dorsal scales reduce to 4 rows on tail opposite third to fifth subcaudal anterior to terminal scute.

Hemipenis forked opposite fifth subcaudal, calyces smooth (1 specimen).

Eight to 9 unmodified maxillary teeth (3 specimens).

Ventrals: males, 123–130 (N=2); female, 146. Subcaudals: males, 29–32 (N=2); female, 14+ (incomplete).

Total length: males, 215–244 mm.; female, incomplete. Ratio of tail to total length, 0.131–0.134 (N=2).

Body and tail dark brown above, each scale with a light network; most scales with a dark central spot; spots frequently unite to form short longitudinal stripes; anteriorly 2 or 3 light spots or vertical bars on side of body; scales of first row whitish, the light area becoming progressively reduced toward rear of body; head dark brown above with obscure lighter spots; dark pigment reaching lip on at least the first 2 supralabials; posterior supralabials with varying amounts of dark pigment; underside of head yellowish with dark brown spots; ventrals and subcaudals with dark lateral margins; tail with a dark mid-ventral streak; otherwise ventral surface immaculate yellow.

Distribution.—Cocos Islands (Fig. 17).

PULO SI LAUT (RMNH 4716A-lectotype, 4716B-syntype; ZMA 10111-syntype).

Calamaria curta Boulenger

Calamaria curta Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **18**, p. 62—South Celebes; 1897, Proc. Zool. Soc. London, **1897**, p. 224, pl. 14, fig. 2; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 160; Smith, 1927, Proc. Zool. Soc. London, **1927**, p. 224; Werner, 1929, Zool. Jahrb., (Syst)., **57**, p. 171; de Haas, 1950, Treubia, **20**, p. 566; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 201.

Holotype.—British Museum (Natural History) 96.4.29.35.

Diagnosis.—Maxillary teeth unmodified; third and fourth supralabials entering orbit; mental touching anterior chin shields; second pair of chin shields meeting in midline.

Description.—Rostral higher than wide, portion visible from above ½ to ⅔ length of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 1 5/6 to 2½ times width of supraocular, about 4/5 length of parietal; parietal 1½ to 1⅔ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye equal to or greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal or second slightly larger than others; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.015–0.029 (2 specimens); tail tapering gradually from base to an extremely long terminal scute; dorsal scales reduce to 4 rows on tail opposite third to sixth subcaudal anterior to terminal scute.

Cloaca of female cardioid (1 specimen).

Seven unmodified maxillary teeth (3 specimens).

Ventrals: male, 156; females, 153–170 (mean 162; N=4). Subcaudals: male, 23; females, 14–17 (mean 15.3; N=4).

Total length: male, 153 mm.; females, 195–307 mm. Ratio of tail to total length: male, 0.105; females, 0.067–0.072 (mean 0.073; N=4).

Color dark brown above, most of dorsal scales with a fine dark network; dorsal scales darker in anterior corners; head dark brown above and on sides with obscure darker spots; supralabials with dark sutures and yellowish ventral borders; head yellow below with dark brown spots; ventrals dark, usually brown in anterior ⅔ and yellowish on posterior edges; small yellowish spots usually present in dark portion of each ventral; subcaudals yellow and brown, usually yellow confined to posterior halves.

Ecological notes.—Smith (1927) found four specimens in and under rotting logs. He stated that their food consisted of earthworms.

Distribution.—Southern Celebes (Fig. 17).

CELEBES: peak of Mount Bonthain, 1500–1800 meters (BM 1926.8.20.167–168; MCZ 25301–02); south Celebes, 610 meters (BM 96.4.29.35—holotype).

Specimens examined—5.

Calamaria acutirostris Boulenger. Figure 19.

Calamaria acutirostris Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **17**, p. 394—Loka, Mount Bonthain, Celebes; 1897, Proc. Zool. Soc. London, **1897**, p. 223, pl. 13, fig. 2; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 86; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 161; Smith, 1927, Proc. Zool. Soc. London, **1927**, p. 224; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171; de Haas, 1950, Treubia, **20**, p. 563; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 199.

Lectotype.—Naturhistorisches Museum Basel 1686, here designated.

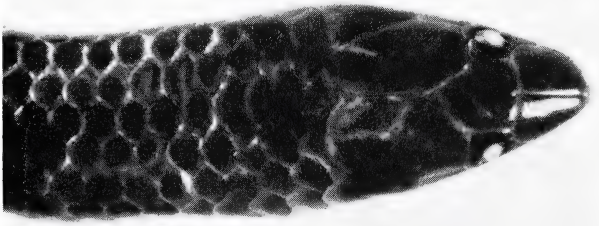

FIG. 19. Paratype of *Calamaria acutirostris* (NMB 1688).

Diagnosis.—Maxillary teeth unmodified; third and fourth supralabials entering orbit; mental touching anterior chin shields; second pair of chin shields not meeting in midline.

Description.—Rostral higher than wide or as wide as high, scarcely visible from above; prefrontal subequal to frontal, touching first 3 supralabials; frontal hexagonal, 2¾ to 3½ times width of supraocular, about ⅔ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal slightly smaller than postocular and larger than preocular; preocular present, neither ocular as high as eye; eye less than or equal to eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first smallest, next 3 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; posterior pair of chin shields not meeting in midline; 4 gulars in midline between anterior chin shields and first ventral.

Body thickness index 0.013–0.070 (10 specimens); tail thick, either tapering gradually or abruptly near end to a point; dorsal scales reduce to 4 rows on tail opposite first to sixth subcaudal anterior to terminal scute.

Hemipenis forked opposite fifth to seventh subcaudal, retractor muscle beginning opposite ninth to twelfth subcaudal, sulcus bifurcate, calyces smooth (5 specimens). Cloaca of female bilobed (2) or bulbous (1).

Ten to 12 unmodified maxillary teeth (9 specimens).

Ventrals: males, 148–162 (mean 154.6; N=18); females, 163–174 (mean 167.6; N=16). Subcaudals: males, 20–24 (mean 21.5; N=18); females, 13–17 (mean 15.2; N=16).

Total length: males, 138–415 mm.; females, 150–447 mm. Ratio of tail to total length: males, 0.086–0.111 (mean 0.094; N=17); females, 0.057–0.069 (mean 0.063; N=16).

Color reddish brown above without markings; dorsal scales without network; head dark brown above; dark pigment ending on a more or less oblique line on supralabials, usually reaching lower edge of anterior supralabials; underside of head yellow with dark spots on anterior infralabials and chin shields; ventrals yellow, usually with a brownish speckling across their anterior edges; subcaudals yellow, edged with brown.

Ecological notes.—Smith (1927) found ten specimens under stones on Mount Bonthain.

Distribution.—Southwestern Celebes (Fig. 17).

CELEBES (NMS 3 [2]; ZMB 15636): Mount Bonthain, Djikoro (CNHM 83161; MCZ 25292–96, 25298; USNM 120810), Loka (BM 96.12.9.61–63—paratypes; NHMW 16714; NMB 1681—lectotype, 1684, 1688–89, 5228–29—all paratypes); Bua Praeng (NHMW 16713: 1–11; SNG 19440).

? Java (ZMB 13947). This specimen was collected by the same collector (Fruhstorfer) and on the same date as SNG 19440. The snake probably came from Celebes.

Specimens examined.—34.

Calamaria schmidti Marx and Inger. Figure 1.

Calamaria schmidti Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 197, fig. 27 — Bundu Tuhan, Mount Kina Balu, North Borneo.

Holotype.—United States National Museum 130240.

Diagnosis.—Maxillary teeth unmodified; four supralabials, second and third supralabials entering orbit.

Description.—Rostral broader than high, portion visible from above about ⅓ length of prefrontal suture; prefrontal squarish, subequal to length of frontal, touching first 2 supralabials; frontal pentagonal, 5 to 6 times width of supraocular, about ⅔ length of parietal; parietal 1⅔ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal larger than eye or postocular; no preocular; postocular not as deep as eye; eye small, diameter ½ eye-mouth distance; 4 supralabials, second and third entering eye, fourth longest, third ¾ or more length of second, first and third equal; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars on midline between second pair of chin shields and first ventral.

Tail ending in a blunt point; dorsal scales reduce to 4 rows on tail opposite the seventh to eighth subcaudal anterior to terminal scute.

Six or seven unmodified maxillary teeth (2 specimens).

Ventrals: males unknown; female, 144 (1 specimen). Subcaudals: females, 14 (2 specimens). Total length of complete female 253 mm.; ratio of tail length to total length: female, 0.075 (1 specimen). The paratype is badly damaged and cannot be measured.

Color purplish gray above, uniform, scales without network; head without markings; supralabials same color as back; anterior infralabials and first pair of chin shields purplish gray, remainder of under side of head yellowish; ventral surface without markings; anterior ventrals yellowish, belly becoming increasingly more purple posteriorly, but lighter than dorsal color; under side of tail darker than belly but slightly lighter than dorsal surface.

Food.—The holotype contained an earthworm.

Distribution.—Mount Kina Balu, North Borneo.

NORTH BORNEO: Mount Kina Balu, Bundu Tuhan, 1370 meters (USNM 130240—holotype), Mount Kina Balu (SU 8568—paratype).

Calamaria lumbricoidea H. Boie. Figure 20.

Calamaria lumbricoidea H. Boie *in* F. Boie, 1827, Isis, **20**, p. 540—Java; Schlegel, 1837, Phys. Serp., pt. 2, p. 27, pl. 1, figs. 14–16; Duméril and Bibron, 1854, Erp. Gén., **7**, p. 89; Günther, 1858, Cat. Colubrine Snakes Brit. Mus., p. 5; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 8; 1865, Icon. Ophid., **10**, pl. 2, fig. 2; Lidth de Jeude, 1890, Notes Leyden Mus., **12**, p. 254; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 333; Boettger, 1886, Ber. Senck. Naturf. Ges., **2**, p. 105; 1894, *in* Semon, Zool. Forsch. Austr., p. 125; 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 83; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 153; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 170; Kopstein, 1930, Treubia, **12**, p. 274; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 183; Inger and Marx, 1962, Syst. Zool., **11**, p. 32.

Calamaria lumbricoidea lumbricoidea, de Haas, 1950, Treubia, **20**, p. 570.

Calamaria vermiformis Duméril and Bibron, 1854, Erp. Gén., **7**, p. 85—"Java" [in error]; Jan, 1862, *loc. cit.*, p. 8; 1865, *loc cit.*, pl. 2, fig. 3; Lidth de Jeude, 1890, *in* Weber, Zool. Ergebn., p. 182; 1922, Zool. Meded., **6**, p. 247; Boulenger, 1894, *op. cit.*, p. 333; 1896, Cat. Snakes Brit. Mus., **3**, p. 646; 1912, Fauna Malay Penin., p. 155; Bartlett, 1895, Sarawak Note Book, no. 1, p. 83; Werner, 1896, Verh. Zool. Bot. Ges. Wien, **46**, p. 17; 1929, *loc. cit.*, p. 170; Boettger, 1898, *loc. cit.*, p. 83; Brown, 1902, Proc. Acad. Nat. Sci. Philadelphia, **1902**, p. 180; Cohn, 1905, Zool. Anz., **29**, p. 545; Baumann, 1913, Zool. Jahrb., (Syst.), **34**, p. 270; Smith, 1916, Jour. Nat. Hist. Soc. Siam, **2**, p. 162; 1925, Sarawak Mus. Jour., **3**, p. 4; 1930, Bull. Raffles Mus., no. 3, p. 58; 1931, *ibid.*, no. 5, p. 27; de Rooij, 1917, *op. cit.*, p. 153; Holtzinger-Tenever, 1920, Arch. Naturg., **85**, p. 86; Mertens, 1924, Zool. Anz., **60**, p. 158; Lonnberg and Rendahl, 1925, Ark. Zool., **17A**, p. 2; de Haas, 1950, *loc. cit.*, p. 575; Tweedie, 1953, Snakes Malaya, p. 49; Marx and Inger, *loc. cit.*, p. 185; Taylor and Elbel, 1958, Univ. Kansas Sci. Bull., **38**, p. 1044.

Calamaria vermiformis vermiformis, Marx and Inger, 1955, *loc. cit.*, p. 187.

Calamaria temmincki Duméril and Bibron, 1854, Erp. Gén., **7**, p. 87—"Sumatra or Borneo"; Günther, 1858, *loc. cit.*, p. 5.

Calamaria grayi Günther, 1858, Cat. Colubrine Snakes Brit. Mus., p. 5—Philippine Islands; Boettger, 1886, *loc. cit.*, p. 105; Boulenger, 1894, *loc. cit.*, p. 338; Taylor, 1922, Snakes Philip. Ids., p. 184; 1922, Philip. Jour. Sci., **21**, p. 204; Werner, 1929, *loc. cit.*, p. 170.

Calamaria dimidiata Bleeker, 1860, Nat. Tijds. Ned. Indie, **21**, p. 295—Java.

Calamaria melanorhynchus Bleeker, *ibid.*—Ampat Lawang, Sumatra.

Calamaria alkeni Bleeker, *ibid.*—Ampat Lawang, Sumtra.

Calamaria flaviceps Günther, 1865, Ann. Mag. Nat. Hist., (3), **15**, p. 90—Sarawak and Borneo.

Calamaria philippinica Steindachner, 1867, Verh. Zool. Bot. Ges. Wien, **17**, p. 514, pl. 8, figs. 4–6—Philippine Islands; Boettger, 1886, *loc. cit.*, p. 105.

Calamaria stahlknechtii Stoliczka, 1873, Jour. As. Soc. Bengal, **42**, p. 119, pl. 11, fig. 2—near Deli, Sumatra; Boulenger, 1885, Ann. Mag. Nat. Hist., (5), **16**, p. 388; 1894, *loc. cit.*, p. 335; Modigliani, 1889, Ann. Mus. Stor. Nat. Genova, (2), **7**, p. 119; de Rooij, 1917, *loc. cit.*, p. 154; Werner, 1929, *loc. cit.*, p. 170; de Haas, 1950, *loc. cit.*, p. 574; Marx and Inger, 1955, *loc. cit.*, p. 206.

Calamaria variabilis Lidth de Jeude, 1890, *in* Weber, Zool. Ergebn., p. 183, pl. 16, fig. 8—Buitenzorg, Java.

Calamaria vermiformis var. *sumatranus* Lidth de Jeude, 1890, Notes Leyden Mus., **12**, p. 18—Deli, Sumatra.

Calamaria bungaroides Werner, 1901, Zool. Anz., **24**, p. 300—type locality unknown; 1929, *loc. cit.*, p. 173; de Rooij, 1917, *loc. cit.*, p. 173; de Haas, 1950, *loc. cit.*, p. 565; Marx and Inger, 1955, *loc. cit.*, p. 200.

Calamaria bruegeli Mertens, 1924, Zool. Anz., **60**, p. 158—central Borneo; de Haas, 1950, *loc. cit.*, p. 565.

Calamaria göringi Vogt, 1925, Zool. Anz., **62**, p. 64—Java; de Haas, 1950, *loc. cit.*, p. 567; Marx and Inger, 1955, *loc. cit.*, p. 202.

Calamaria goeringi, Werner, 1929, *loc. cit.*, p. 171; Brongersma, 1930, Treubia, **12**, p. 302.

Changulia lumbricoidea, de Haas, 1941, Treubia, **18**, p. 369.

Calamaria gracilis (non Boulenger), Angel, 1941, Bull. Mus. Nat. Hist. Nat., (2), **13**,, p. 411.

Calamaria vermiformis grayi, Marx and Inger, 1955, *loc. cit.*, p. 188; Leviton, 1963, Proc. Calif. Acad. Sci., **31**, pp. 379, 389, 393, 404.

Lectotype.—Rijksmuseum van Natuurlijke Historie 10543 (ex 42).

Taxonomic notes.—Duméril and Bibron did not compare *vermiformis* with the very similar species *lumbricoidea.* Boulenger (1894) differentiated these two forms solely on the basis of eye size, which he said was smaller than the eye-mouth distance in *lumbricoidea* and equal to that distance in *vermiformis.* De Rooij (1917) merely copied Boulenger's descriptions. In his descriptions Boulenger stated that the ventral coloration of *lumbricoidea* was whitish whereas that of *vermiformis* was highly variable, ranging from uniform yellow through increasing amount of black transverse bands to uniform black.

Our examination of 375 specimens from all parts of the combined ranges of *lumbricoidea* and *vermiformis* convinces us of their conspecificity. We confirm Boulenger's observation of the range of ventral coloration. We cannot, however, confirm Boulenger's observations on eye size; Javanese snakes agreeing in all details with the type series of *lumbricoidea* have eye diameters ranging from slightly smaller to larger than the eye-mouth distance. Snakes from Borneo, indistinguishable from the type series of *vermiformis,* show the same variation in eye size. Both sets of specimens have the same distinctive round snout and a relatively thick body. Especially significant is the fact that only these two nominal forms out of the entire genus show ontogenetic variation in coloration of the head (see below).

The type locality of both *vermiformis* and *lumbricoidea* is Java. All of Boie's material was from Java and subsequent collecting has turned up all of his species of *Calamaria* on Java. Consequently the type locality of the older name, *lumbricoidea,* is correctly given. Numerous specimens agreeing with the types of *lumbricoidea* in those few characters by which these two type series differ (see *Geographic variation*) have been collected over a long period of time on Java by various collectors.

Seven specimens with the characteristics of *vermiformis* (i.e., banded ventrally) have been reported from Java. Of these only one (MHNP 39-187) is reported from a specific locality, Batavia (=Jakarta). As none of the recent large Javanese collections of *Calamaria* include *vermiformis,* which is one of the common forms in other parts of the generic range, we doubt that this color form occurs on Java.

The detailed original description and figures of *stahlknechti* agree in counts and coloration with typical Sumatran specimens of *lumbricoidea.* Snakes from Nias identified by Boulenger (1894) and de Rooij (1917) as *stahlknechti* have been examined and are also *lumbricoidea.*

The holotype of *göringi* does not differ from Javanese *lumbricoidea.*

Our examination of the holotype of *bruegeli* confirms our previous opinion (Marx and Inger, 1955) that it is synonymous with *vermiformis* and therefore with *lumbricoidea.*

The original description of *Calamaria bungaroides* fits juvenile Bornean and Sumatran *lumbricoidea* exactly.

We have examined the types of *temmincki, dimidiata, melanorhynchus, alkeni, flaviceps, vermiformis* var. *sumatranus,* and *variabilis* and agree with Boulenger (1894) that they are synonymous with *lumbricoidea* and *vermiformis* of Boulenger.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 4 or 5 scales and shields; belly yellow with black crossbars wider than width of one ventral.

Populations of *lumbricoidea* from Java and parts of Sumatra have immaculate light bellies. Javanese *lumbricoidea* are distinguished from all other species known from that island by the other characters mentioned in the diagnosis. Those characters also distinguish the light-bellied Sumatran *lumbricoidea* from all other Sumatran *Calamaria* except *albiventer.* The last has two lateral light stripes which differentiate it from *lumbricoidea.*

Description.—Rostral wider than high, or higher than wide, portion visible from above about half length of prefrontal suture; prefrontal equal to or slightly shorter than frontal, touching first 2 supralabials; frontal hexagonal, 1½ to 2½ times width of supraocular, about ¾ to $^5/_6$ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 4 or 5 shields and scales; nasal smaller than postocular; preocular present, higher than postocular; postocular usually not as high as eye; eye smaller than, equal to, or greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal or third the smallest; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields usually meeting in midline; usually 3 gulars in midline between posterior chin shields and first ventral (see *Geographic variation* below).

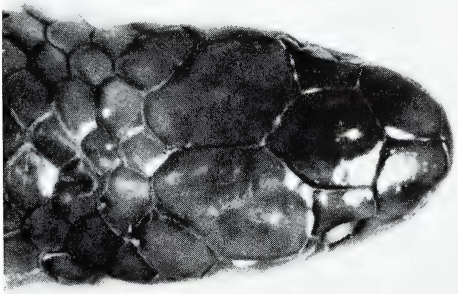

Fig. 20. *Calamaria lumbricoidea* (NHMW 16698:3).

Body thickness index 0.012–0.074; tail thick, tapering abruptly near tip to sharp point; dorsal scales reduce to 4 rows on tail opposite first to eleventh subcaudal anterior to terminal scute.

Hemipenis variable (see *Geographic variation*). Cloaca of female bilobed, bulbous, or cardioid, not varying geographically (Inger and Marx, 1962).

Nine (1 specimen), 10 (19) or 11 (2) modified maxillary teeth.

Ventrals: males, 144–196 (mean 172.0; N=132); females, 137–229 (mean 190.8; N=116). Subcaudals: males, 17–27 (mean 21.5; N=134); females, 13–21 (mean 16.3; N=118).

Total length: males, 149–498 mm.; females, 120–642 mm. Ratio of tail to total length: males, 0.063–0.114 (mean 0.080; N=126); females, 0.039–0.083 (mean 0.056; N=113).

Color dark brown or black above, with or without narrow, light stripes; scales without network; first one or two scale rows yellow;

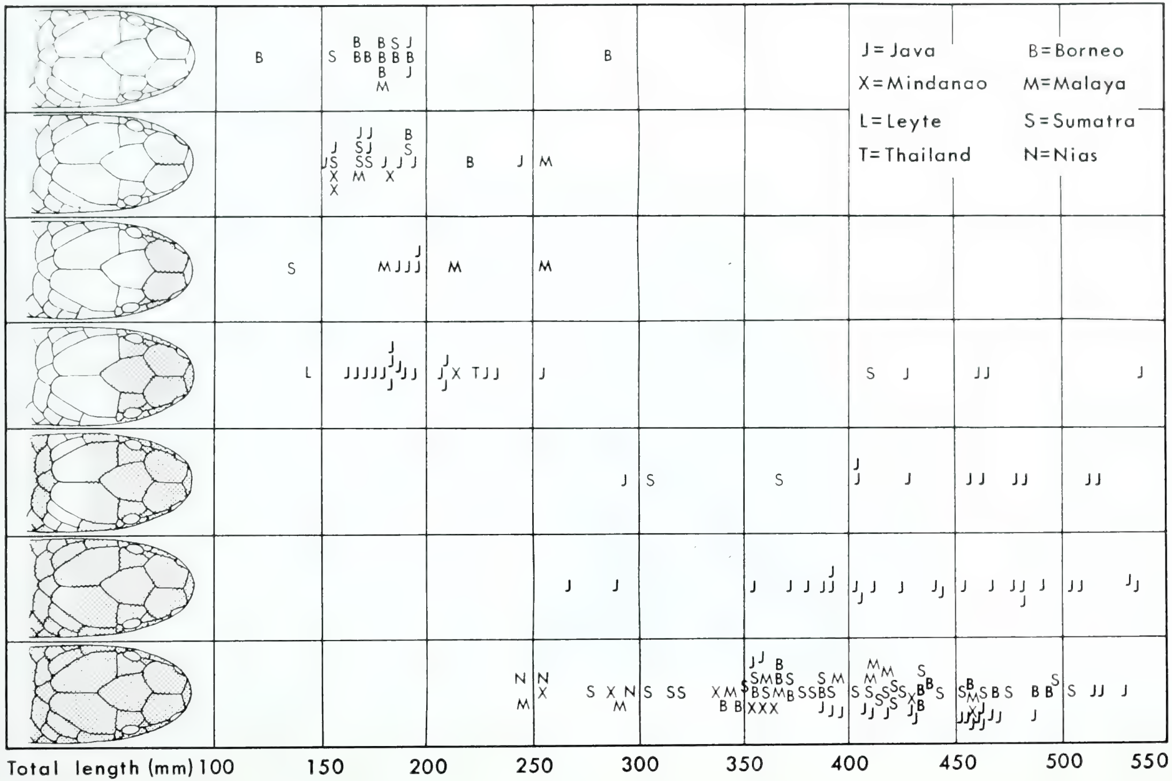

FIG. 21. Ontogenetic variation in head coloration in *Calamaria lumbricoidea*. Brown or black areas stippled.

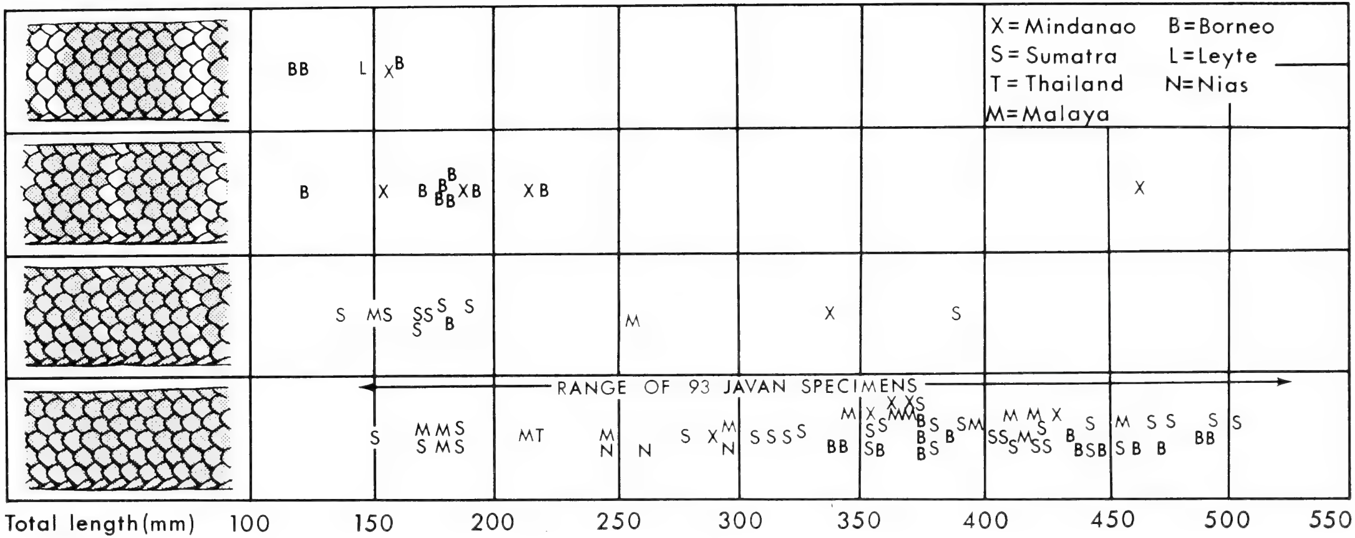

FIG. 22. Ontogenetic and geographic variation in body pattern of *Calamaria lumbricoidea*. Yellow areas not stippled.

ventral surface yellow, with or without black crossbands (see *Ontogenetic variation* and *Geographic variation*).

Ontogenetic variation.—The heads of juveniles (up to about 200 mm., total length) are yellow in preservative whereas those of adults are dark brown or black. Darkening of the head begins on the snout and gradually spreads to cover the entire head (Fig. 21).

Juveniles of most populations have yellow bands across the dorsum. These bands are one-half to two scales wide (Fig. 22).

Geographic variation.—Figure 21 suggests that Bornean juveniles tend to have lighter heads than do those from Java. Adults from Java often retain a narrow light band or pair of light spots on the rear of the parietals. Such spots or bands rarely occur in adults in other parts of the range (Fig. 21).

The yellow dorsal crossbands are usually less than one scale wide and usually interrupted in juveniles from western Sumatra and western Malaya. In juveniles from Borneo and the Philippine Islands these bands are usually continuous and one to two scales wide. Yellow crossbands are absent in juveniles from Java, eastern Sumatra, and central Malaya (Fig. 22).

Tweedie (1953) states that longitudinally striped *lumbricoidea* are confined to high altitudes and uniform brown snakes to low altitudes. The striped Malayan snakes examined by us come from 1,300 to 1,400 meters above sea level and non-striped ones from 500 to 1,350 meters. Limiting observations to Malaya might lead to the conclusion that the variation is altitudinal. However, all *lumbricoidea* from Java (350 to 1,400 meters) and Borneo (50 to 1,430 meters) are non-striped though they span the altitudinal range of the Malayan specimens. All *lumbricoidea* from the Philippine Islands (sea level to 850 meters) are longitudinally striped.

Clearly this aspect of dorsal pattern varies geographically rather than altitudinally (Table 21). The non-striped Malayan snakes occur along the western edge of the peninsula and the striped ones farther inland. In Sumatra non-striped snakes occur along the eastern coast and striped ones on the west.

The ventrum in *lumbricoidea* varies from uniform yellow to almost solid black. Black on the belly usually takes the form of black crossbands that occupy 2 to 4 adjacent ventrals separated by varying numbers of yellow scales. In three specimens the belly is entirely black. Some specimens without black crossbands have black speckling that varies from a few tiny spots on scattered ventrals to a more or less continuous dark stripe midventrally. Geographic variation

TABLE 21.—Frequency Distribution of Dorsal Patterns and Number of Gulars in Samples of *Calamaria lumbricoidea*.

		Dorsal pattern		No. of gulars	
Localities		Striped	Uniform	*3*	*4*
Thailand			1		1
Malaya:	Pahang	8		7	1
	Perak		4		4
	Selangor		4		3
	Johore		2		2
Sumatra:	Padang area	20	3	25	
	Deli		8	1	7
	Palembang		1	1	
	Si Rambè		1		1
	Bindjay		2		2
	Langhat		2		2
	Ophir District	1	1	1	1
Nias			6	1	5
Borneo:	Kina Balu		13	13	
	Lawas		1		1
	Pa Brayong		1	1	
	Baram District		4	2	2
	Niah		2	1	1
	Matang		1	1	
	Batu Song		1	1	
	Tandjong		2		2
	Mahakam		2	2	
	Sandakan		1	1	
Java			125	125	
Natuna			1		1
Mindanao		14		13	1
Bohol		1		1	
Basilan		1		1	
Leyte		1		1	

of ventral coloration is shown in Table 22. The belly pattern shows not only inter-island variation, but also variation within Sumatra as a comparison of the Deli and Padang specimens indicates.

Populations from the Philippine Islands, Borneo, Java, western Sumatra, and central Malaya have 3 mid-ventral gulars whereas 4 is the common number elsewhere (Table 21).

Within islands the number of ventrals varies to a remarkable extent (Tables 23 and 24). Yet at any given locality, *lumbricoidea* follows the common pattern of this genus by having relatively little individual variation (see p. 24). For example, in the Kina Balu sample the range of ventrals is 170–180 in seven females and 154–165 in seven males or only a fraction of the range for the entire Bornean sample. Despite much overlap, the populations from Java and the Philippine Islands have higher ventral counts than do those from other areas.

TABLE 22.—Frequency Distribution with Respect to Amount of Black on Ventrals of *Calamaria lumbricoidea.*

Locality	All yellow	Few half ventrals	Single ventrals	Pairs of black ventrals, separated	Pairs of black ventrals, close	Three to four ventrals	Almost all black	All black
Thailand	..	..	..	..	1	..	..	..
Malaya	..	..	1	..	2	7	6	1
Sumatra: no other data	3	1	1	2	1	1	1	..
” Padang	3	..	3	1	7	..	..	..
” Deli	1	..	..	1	2	2	2	..
” Langkat	..	..	..	..	1	..	..	..
” Palembang	..	1	..	..	..	..	..	..
” Si Rambe	..	..	..	..	1	..	..	..
” Total	6	2	4	4	15	3	4	2
Nias	6	..	..	..	..	..	..	..
Borneo	..	..	2	..	17	6	1	..
Java	130	..	..	..	..	..	..	..
Mindanao	..	..	..	..	5	7	2	..
Bohol	..	..	..	..	..	1	..	..
Basilan	..	..	..	..	1	..	..	..
Leyte	..	..	.	..	1	..	..	..

Similar geographic variation—slight differences between areas with extensive overlap—is shown by subcaudal counts, the position of the reduction to four dorsal scale rows, and the ratio of tail length to total length (Tables 25 and 26).

The hemipenis of *lumbricoidea* shows variation not seen in other species of *Calamaria* (Inger and Marx, 1962). Males from the mainland, Sumatra, Nias, and Java are alike in having the hemipenis forked beginning between the second and sixth subcaudals (as is characteristic of the genus) and in having both rami covered with papillate calyces; the sulcus forks at the base and a branch runs to the apex of each fork (as in Fig. 4F of Dowling and Savage, 1960).

The same type of hemipenis was found in males from North Borneo and Sarawak. However, males from widely separated localities in Borneo have undivided hemipenes that have smooth calyces; the sulcus is bifurcate in these simple hemipenes. Aside from the range of variation among these Bornean specimens, the striking aspect is the lack of variation within a local population, such as that of Mount Kina Balu.

Characters that vary geographically in *lumbricoidea* are not associated in any fixed way with the result that geographic variation in one character does not coincide with that of another (Table 27). If subspecies were named they would have to be based on a single character and the choice of that character would be arbitrary.

Distribution.—From southern Thailand to Java, Borneo, and Leyte (Fig. 72).

THAILAND: Bangkok (UMMZ 65331).

MALAYA: Perak: Gunong Kledong (NMS unnumbered), Larut Hills (BM 1900.6.14.22), 1370 meters (NMS unnumbered), Taiping (ZMB 26457). Pahang: Fraser's Hill (NMS 30229, 4 unnumbered), Cameron Highlands, Kuala Terla (CNHM 72374), Cameron Highlands, Tanah Rata, 1400 meters (NMS 2 unnumbered). Selangor: Kepong Forest Reserve (NMS 13880, 30462), 640 meters (NMS 9474), Kepong, Bukit Lagong (NMS 8827). Johore: Gunong Pulai (NMS 2 unnumbered).

NIAS (BM 84.12.31.7, 84.12.31.8[2]; RMNH 4865). Gunong Sitoli (MCG 30381); west Nias (ZMA 10234).

SUMATRA (AMNH 2879; BM 62.12.4.123—syntype of *alkeni;* NHMW 16699[2]; NMB 10769; RMNH 33[2], 43, 78, 5806[3], 1 unnumbered; USNM 56439). East coast of Sumatra (BM 93.6.5.3);

TABLE 23.—Frequency Distribution of Ventral Counts in Males of *Calamaria lumbricoidea.*

	Class centers																	
	145	*148*	*151*	*154*	*157*	*160*	*163*	*166*	*169*	*172*	*175*	*178*	*181*	*184*	*187*	*190*	*193*	*196*
Thailand											1							
Malaya (total)				1	2	1	1	1		1								
Pahang				1	2	1	1											
Perak								1		1								
Sumatra (total)					1	3	8	9	5	1	2		2		1	2	1	1
Bukit Tingi					1		2	3	2									
Padang						2	2		1							1		
Kaba Wetan																1	1	1
Nias		3	1	1														
Greater Natuna					1													
Borneo (total)	2	1	2	2	3	2	3	3	1	2		1	1					
Kina Balu				1	3	2		1										
Java (total)										1	1	2	20	10	3	4	1	2
Tjikadjang												1	16	8	1			
Philippine Islands								2		2	3							

TABLE 24.—Frequency Distribution of Ventral Counts in Females of *Calamaria lumbricoidea.*

	Class centers																					
	137	*160*	*163*	*166*	*169*	*172*	*175*	*178*	*181*	*184*	*187*	*190*	*193*	*196*	*199*	*202*	*205*	*208*	*211*	*214*	*217*	*220*	*229*
Malaya (total)					1	1	2	2	2	2													
Pahang					1	1	1																
Perak								1	1														
Sumatra (total)							3	6	3	1	3	2	4			1		2	2		1		
Bukit Tingi							2	1	1				1										
Padang								1					1			1							
Kaba Wetan																		1	2		1		
Nias			1																				
Borneo (total)	1	2		2	3	1	3	1	1	2					2								
Kina Balu					1	1	3	1	1														
Java (total)														2	8	14	5	5		1		1	
Tjikadjang														1	8	13	5	3					
Philippine Islands											1	1	5	2	3	1		1					1

Si Rambè (MCG 30376). Sumatera Utara: Bindjai (ZMH 2466[2]), Deli (BM 89.12.16.108; NHMW 16817; RMNH 1228[2]—syntypes of *vermiformis* var. *sumatrana*, 6636, 1 unnumbered; SNG 19390, 19392; ZMA 10227, 10229, 10235), Langkat (MCZ 37769–70). Sumatera Tengah: Bukit Tingi (BM 1928.2.18.23–30; RMNH 5806[2]; ZMA 10228[3]), Padang (BM 83.5.24.4–6; MCZ 20971; NHMW 16700[2], 16701–02; RMNH 511, 535), Batu Sangkar (RMNH 4861), Solok (NMB 1703), Ophir district, Sukamananti, 200 meters (RMNH 5806), Ophir district, Tanano-Talu, 1000 meters (RMNH 5806), Kaba Wetan (USNM 70945–51). Sumatera Selatan: Palembang (ZMA 10232), Ampat Lawang (BM 63.12.11.184; RMNH 3976—syntype of *melanorhynchus*). ?Sumatra (RMNH 41).

GREAT NATUNA (BM 95.5.1.76).

TABLE 25.—Frequency Distribution with Respect to Certain Characters in Males of *Calamaria lumbricoidea*.

Subcaudals

	17	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*
Mainland				1	1	3	1	1		1	1
Nias				1	2	2					
Sumatra			1	7	8	14	6	1			
Borneo			2		4	2	7	5	1	2	
Philippine Islands						2	1	2	1		1
Java	1	1	14	20	7	1					

Position of reduction to four dorsal scale rows[1]

	10	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*25*
Mainland					2	1		3		3				
Nias					1		3		1					
Sumatra		1	2	3	3	8	7	4	3	2	3			
Borneo	1				1	4	2	6	3		3	1	1	1
Philippine Islands						1	1		8		2			
Java			1	2	6	7	15	9	2					

Tail ratio[2]
Class centers

	54	*63*	*68*	*73*	*78*	*83*	*88*	*93*	*98*	*103*	*108*	*113*
Mainland						1	3	1	1			2
Nias						1	2	2				
Sumatra			2	7	7	13	2	2				
Borneo					5	1	4	4	2	2	2	1
Philippine Islands							3	2		1		
Java	1	10	24	7	2							

[1] Position given in terms of subcaudals counted from vent.

[2] Ratio in thousandths of total length.

TABLE 26.—Frequency Distribution with Respect to Certain Characters in Females of *Calamaria lumbricoidea.*

	Subcaudals								
	13	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*
Mainland			1	2	3	2			2
Nias			1						
Sumatra	2	2	1	10	9	4	1		
Borneo		3		2	3	7	1	2	1
Philippine Islands		2	3	2	3	4		1	
Java	2	11	16	13	1				

	Position of reduction to four dorsal scale rows[1]												
	6	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*
Mainland				1		1	5	1			1	1	
Nias						1							
Sumatra	1	1			7	3	9	1	1	3			1
Borneo	1	1	1	2		3	2	5		1	1	1	
Philippine Islands	1	1			3	3	1	3	3			1	
Java		1	4	5	7	11	5	3		1			

	Tail ratio[2] Class centers									
	39–40	*43*	*48*	*53*	*58*	*63*	*68*	*73*	*78*	*83*
Mainland				2	2	2	2	1	1	
Nias						1				
Sumatra			1	9	10	7				
Borneo				1	1	3	4	4	2	3
Philippine Islands			1	2	7	4				
Java	2	15	18	3						

[1] Position given in terms of subcaudals counted from vent.

[2] Ratio in thousandths of total length.

SARAWAK (BM 45.10.2.45—syntype of *flaviceps*): First Division: Bidi (SM Cd.5.26.1c; Cd.5.26.15b), Kuching (SM Cd.5.26), Matang (BM 73.3.4.23). Second Division: Saribas (SU 8575). Fourth Division: Niah, Rumah Sigi (CNHM 129005), Niah, Kuala Sakoloh (CNHM 129006), Niah (CNHM 131620–27), Mount Batu Song, 300 meters (BM 92.10.7.8), Baram district (BM 97.3.4.5, 1902.2.11. 25.16–17; NHMW 16992:1). Fifth Division: Lawas (CNHM 67278), Lawas, Sungei Usop (SM Cd.5.26.1d), Pa Brayong (CNHM 71646).

NORTH BORNEO: Ranau District: Mount Kina Balu (MHNP 89–193), Bundu Tuhan, 1370 meters (USNM 130252). Kota Belud District: Mount Kina Balu, Tenompok, 1430 meters (MCZ 43563), Kiau, 915 meters (BM 1929.12.22.110–111; MCZ 43564–65; NMS 16817), Kenokok River, 1000 meters (MCZ 43566–69; UMMZ 82829[2]). Sandakan District: Sandakan (CNHM 15003).

TABLE 27.—Summary of Geographic Variation in *Calamaria lumbricoidea*.

	Dorsal coloration	Ventral banding[1]	Juvenile banding[2]	Gulars	Ventrals[3]		Subcaudals[3]		Reduction[3]		Hemipenis	
					♂	♀	♂	♀	♂	♀	Shape	Calyces
Thailand	uniform	heavy		4		176		23		18	forked	
Malaya,												
central	striped	heavy	absent	3	154–162(158)	169–174(172)	21–24(22)	17–18(18)	15–20(17)	10–13(12)	forked	papillate
western	uniform	heavy	narrow	4	165–171(169)	175–184(180)	20–27(24)	15–21(18)	16–20(19)	12–18(14)	forked	papillate
Sumatra												
eastern	uniform	heavy	absent	4	164–193(170)	177–207(188)	20–23(21)	14–17(16)	13–21(17)	7–16(12)	forked	papillate
western	striped	light-absent	narrow	3	158–191(170)	176–217(193)	19–24(22)	16–19(17)	12–19(16)	11–18(14)	forked	papillate
Nias	uniform	absent		4	147–153(150)	164	20–22(21)	15	15–17(17)	12	forked	papillate
Java	uniform	absent	absent	3	172–196(183)	197–220(203)	17–21(20)	13–18(15)	12–18(15)	8–16(12)	forked	papillate
Natuna	uniform	absent		4	157		21		15			
Borneo	uniform	heavy	wide	3–4	144–181(160)	137–200(173)	19–26(23)	14–21(17)	11–25(19)	7–18(13)	forked-simple	papillate-smooth
Philippine Islands	striped	heavy	wide	3	165–176(171)	188–229(198)	22–27(24)	14–20(17)	16–21(19)	7–18(12)	forked	smooth

[1] Light=second to fourth columns of Table 22; heavy=fifth to eighth columns of Table 22.

[2] Wide=bands one to two scales wide; narrow=less than one scale wide.

[3] Means in parentheses.

Indonesian Borneo: Boven Mahakam (RMNH 2 unnumbered), Tandjong (BM 96.2.17.11–12), southeast Borneo (SMNS 3493, 3493a, 3497; ZMH 2421).

Borneo (BM 56.9.27.9—syntype of *flaviceps*, 72.2.19.55, 1 unnumbered; USNM 49802); central Borneo (SNG 19389—paratype of *bruegeli*); north Borneo (NHMW 16992:2–3; ZMB 13110).

Basilan: near Isabela (MCZ 43469).

Mindanao: Zamboanga Province: Zamboanga City (CAS 15291), Zamboanga (City?) (CAS 62030). Cotabato Province: Mount Malindang, Gumay (CNHM 96529), Cotabato (NMB 8513), Saub (MCZ 25778–80; USNM 120811), Cotabato coast (ZMA 10236). Misamis Province: Lake Lanao (CAS 15286–89), Lanao, Lumbatan (CNHM 15010). Davao Province: Mount Apo, Todaya, 855 meters (CNHM 53373).

Negros: Negros Oriental: Dumaguete (SU 15952).

Bohol (NHMW 16815).

Leyte: Cabalian (MCZ 25781).

Samar: Osmera (USNM 122215).

Philippine Islands (BM 1946.1.2.17, 1946.1.2.21—syntypes of *grayi;* ZMB 5446).

Java (BM 44.2.32.65, 66.8.14.344, 70.6.7.46, 73.5.3.26; CNHM 83163; MHNP 165; NHMW 16698[6], 16816, 2 unnumbered; NMS 253; RMNH 10419[4], 10543—lectotype of *lumbricoidea,* 42[2]—paratypes of *lumbricoidea;* SNG 19388, 19393; ZMA 10233[2]; ZMB 1552, 4069, 4117, 6936, 8545—holotype of *göringi*, 8758, 10261; ZMH 4651-4652, 5880). M. Pangherango (MCG 30457); ?Tjikorai (NMS 5). Djawa Barat: Benkang near Serang (AMNH 71513), Djakarta (NMS 544), Bogor (RMNH 4327—holotype of *variabilis;* SNG 19386, Medamendoeng Peak, between Bogor and Sindanglaja (MHNP 95–52[2]), Sindanglaja (MCZ 7523), Bandung, 800 meters (RMNH 7463[3], 1 unnumbered), Mount Gede, Tjibodas, 1450 meters (RMNH 8604), Rarahan, near Tjibodas (MCG 6780, 30378), Mount Garut (NHMW 16697:1), Mount Garut, plantation Dajeuhmanggoeng (RMNH unnumbered), Tjikadjang, 900 meters (RMNH 6833[4], 126 unnumbered), Tjusurupan (SNG 19387, 19391), Tasikmalaja, 350 meters (NHMW 16697:2). Djawa Tengah: Wonosobo, Kepil, 550 meters (RMNH 8555), Wonosobo, Selomojo, 600 meters (RMNH unnumbered), Wonosobo, Tlogodjati, 1000 meters (RMNH unnumbered).

Questionable localities: Java (BM 61.8.12.44, 63.12.11.171—holotype of *dimidiata;* MHNP 174 and 3300[2]—syntypes of *vermiformis;* ZMB 4118—syntype of *vermiformis*). Java: Batavia (MHNP 39-187; RMNH 80—holotype of *temmincki*). Java: Bandung (RMNH co.118). Dutch Indies (MNHP 12-51, 12-52, 12-54; RMNH 3975). Malayan Archipelago (NHMW 16694). Ternate (BM 78.1.31.8-9). No data (RMNH unnumbered).

Specimens examined.—386

Calamaria griswoldi Loveridge. Figure 23.

Calamaria lumbricoidea griswoldi Loveridge, 1938, Proc. Biol. Soc. Washington, **51**, p. 43—Luidan River, Bundu Tuhan, Mount Kina Balu, North Borneo; de Haas, 1950, Treubia, **20**, p. 570.

Calamaria griswoldi, Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 183.

Holotype.—Museum of Comparative Zoology 43580.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; color blackish brown above with a narrow white line between successive scale rows; immaculate yellowish white below.

Description.—Rostral wider than high, portion visible from above ⅔ length of prefrontal suture; prefrontal $^5/_6$ length of frontal, touching first 2 supralabials; frontal hexagonal, 1⅓ to 2 times width of supraocular, about ⅔ to ¾ length of parietal; parietal 1⅔ to 2 times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye equal to or slightly greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.017-0.039 (5 specimens); tail thick, tapering from base to a sharp point (Fig. 10B); dorsal scales reduce to four rows on tail opposite ninth to thirteenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth subcaudal; sulcus spermaticus forked; calyces papillate (2 specimens).

Nine to 10 modified maxillary teeth (4 specimens).

Ventrals: males, 155-179 (mean 168.5; N=6); females, 183-192 (mean 187.2; N=5). Subcaudals: males, 16-18 (mean 16.7; N=6); females, 13-16 (mean 14.5; N=4).

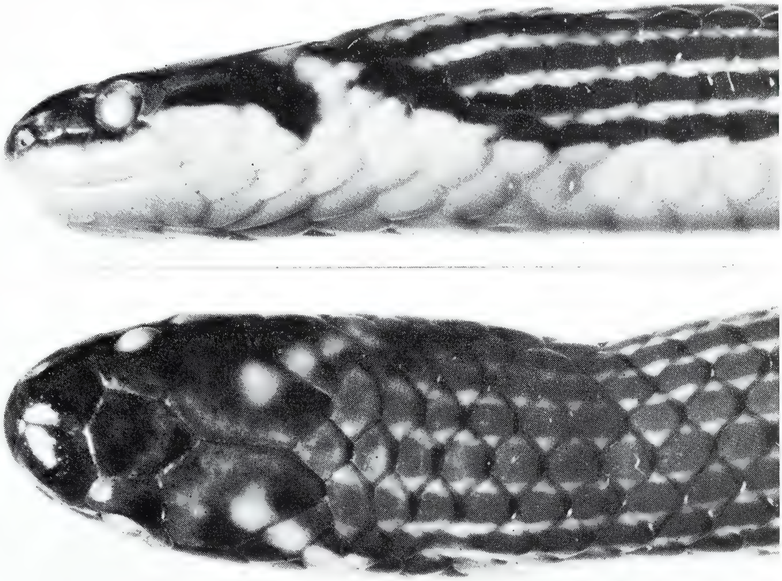

FIG. 23. *Calamaria griswoldi* (NMS R18949).

Total length: males, 192–425 mm.; females, 375–488 mm. Ratio of tail to total length: males, 0.059–0.068; (mean 0.063; N=6); females, 0.048–0.056 (mean 0.052; N=4).

Color dark brown above; dark portion of scales without network; blackish brown stripes occupying central ⅔ of each scale row above the first, yellowish stripes on edges on adjacent scale rows; scales of first row yellow, immaculate in anterior part of body, usually each scale with a small dark spot in posterior half of body; head dark brown above; supralabials yellow in lower ⅔; head below immaculate yellow; an oblique light bar running forward from gular region onto rear of parietals; ventrals immaculate yellow; subcaudals yellow, usually a faint zig-zag dark line mid-ventrally.

Distribution.—Highlands of northwestern Borneo (Fig. 72).

NORTH BORNEO: Ranau District: Ranau (USNM 134114), Mount Kina Balu (BM 5.11.7–25), Lumu Lumu, 1525 meters (BM 1929.12.22.112), Bundu Tuhan, 1370 meters (CNHM 72434; USNM 130238), Luidan River, near Bundu Tuhan (MCZ 43580—holotype, 43581—paratype). Kota Belud District: Tenompok, 1430 meters (NMS 18949, 1 unnumbered). Western North Borneo (SM Cd. 5.26.c–d).

SARAWAK. Fourth Division: Kelabit Plateau (SM unnumbered).

Specimens examined.—12.

Calamaria albiventer Gray. Figure 24.

Changulia albiventer Gray, 1834, Ill. Ind. Zool., **2**, pl. 86, figs. 6–9—Penang Island.

Calamaria albiventer, Günther, 1858, Cat. Colubrine Snakes, p. 4; 1864, Rept. Brit. Ind., p. 197; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 336; 1912, Fauna Malay Penin., Rept. and Batr., p. 156; Flower, 1896, Proc. Zool. Soc. London, **1896**, p. 886; 1899, *ibid.*, p. 674; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 170; Smith, 1930, Bull. Raffles Mus., no. 3, p. 58; Tweedie, 1953, Snakes Malaya, p. 50; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 199; Batchelor, 1958, Malaya Nat. Jour., **12**, p. 107.

Calamaria indragirica Schenkel, 1901, Verh. Ges. Basel, **13**, p. 164, fig. 3—Indragiri, Sumatra; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 154; Werner, *loc. cit.*, p. 170; de Haas, 1950, Treubia, **20**, p. 568; Marx and Inger, *loc. cit.*, p. 202.

Calamaria ornata Werner, 1909, Mitt. Naturh. Mus. Hamburg, **26**, p. 229, fig. 6—Sungei Lalak, Indragiri, Sumatra; de Rooij, *loc. cit.*, p. 178; de Haas, *loc. cit.*, p. 572; Marx and Inger, *loc. cit.*, p. 204.

Syntypes.—British Museum (Natural History) 1946.1.2.10, 1946.1.2.18.

Taxonomic notes.—The striking color patterns of *indragirica* and *ornata* are identical to that of *albiventer*. As the counts and scale proportions also agree, we are putting the two Sumatran names in the synonymy of *albiventer*.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; body with 4 narrow light stripes.

Description.—Rostral broader than high, portion visible from above about ⅔ length of prefrontal suture; prefrontal ¾ length of frontal, touching first 2 supralabials; frontal hexagonal, 1⅔ to 2 times width of supraocular, about $^5/_6$ length of parietal; parietal 1½ times length of prefrontal; paraparietal usually surrounded by 5 shields or scales; nasal smaller than or equal to postocular; preocular present, neither ocular as high as eye; greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.026 (1 specimen); tail tapering gradually from base, abruptly tapering at tip to a sharp point; dorsal scales reduce to 4 rows on tail opposite fifth to eighth subcaudal anterior to terminal scute.

Cloaca of female bilobed (1 specimen).

Nine modified maxillary teeth (3 specimens).

Ventrals: males, 143–144 (N=2); females, 147–162 (mean 156.4; N=10). Subcaudals: males, 21–22 (N=2); females, 15–19 (mean 17.0; N=10).

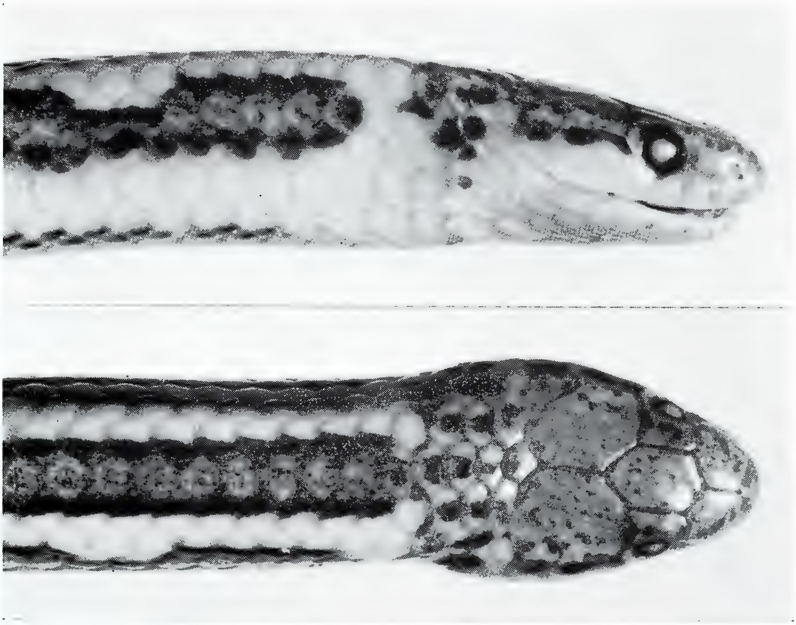

FIG. 24. *Calamaria albiventer* (CAS 14940).

Total length: males, 205 mm. (N=2); females, 170–361 mm. Ratio of tail to total length: males, 0.088–0.093 (N=2); females, 0.047–0.088 (mean 0.066; N=9).

Color of body brown above; two pairs of light longitudinal stripes; lower half of first scale row and adjacent edges of ventrals brown; adjacent halves of first and second scale rows yellowish; a broad dark stripe on upper half of second scale row, all of third and fourth rows, and lower half of fifth row; this dark band sometimes split by a lighter brown stripe formed by light speckling on adjacent halves of third and fourth scale rows; yellowish stripe on adjacent halves of fifth and sixth scale rows; a dark stripe on vertebral scale row and adjacent halves of sixth rows; top of head light brown with a dark network or dark spots; upper third or half of supralabials brown; remainder of supraliabals and underside of head yellowish, usually with dark spots on infralabial sutures; ventrals yellow except for dark lateral edges; underside of tail yellowish with a dark median stripe.

In life reddish brown above; upper light stripe red, lower light stripe bluish white; both light stripes edged with black; underside of head lemon yellow shading into red on neck; underside of body and tail bright red (Flower, 1899, p. 674).

Geographic variation.—Two Sumatran specimens (syntypes of *indragirica*) have 147 and 148 ventrals and 19 subcaudals. One of these snakes is a female; the second was too desiccated to determine the sex. The third Sumatran animal (holotype of *ornata*) has 148 ventrals and 17 subcaudals (Werner, 1909b, p. 229); sex was not given. If these 3 snakes are females, Sumatran females have lower ventral and higher subcaudal counts than females from Malaya (156–160; 15–17).

Distribution.—Western Malaya and east-central Sumatra (Fig. 72).

MALAYA: Penang Island (BM 1946.1.2.10 and 1946.1.2.18—syntypes, 60.3.19.1269[2], 98.9.22.39). Perak: Larut Hills, 1370 meters (NMS unnumbered). Province Wellesley (BM 96.6.25.28).

SINGAPORE (CAS 14940).

SUMATRA: Sumatera Tengah: Indragiri (NMB 1697–98—syntypes of *indragirica*), Indragiri, Sungei Lalak (holotype of *ornata;* not examined).

?India (BM 2 unnumbered).

Specimens examined.—12.

Calamaria hilleniusi new species. Figure 25.

Holotype.—Zoologisch Museum Amsterdam 10078, a male from Samarinda, Indonesian Borneo.

Paratypes.—Sarawak Museum unnumbered, a female from northwestern Borneo; Agriculture Department, Sabah, No. 72, (male) and, Chicago Natural History Museum 142088, (female) both from Tuaran, Tuaran District, Sabah (=North Borneo).

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 5 shields and scales; eye about ⅔ eye-mouth distance; dorsal scales without network.

Description.—Rostral wider than high, portion visible from above equals half length of prefrontal suture; prefrontal equals length of frontal, touching first 2 supralabials; frontal hexagonal, 2½ to 3 times width of supraocular, about ¾ length of parietal; parietal 1⅓ to 1½ times length of prefrontal; paraparietal surrounded by 5 scales and shields; nasal oriented laterally, equal to postocular; preocular present; both oculars as high as eye; eye about ⅔ eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, fourth almost as long as fifth along ventral border, dorsal margin of fourth labial half of its ventral margin; first 4 supralabials subequal along labial border; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.041–0.052 (2 specimens); tail tapering gradually from base to a point; dorsal scales reduced to 4 rows on tail opposite third to ninth subcaudal anterior to terminal scute.

Hemipenis in holotype too small for accurate description, sex determined by examination of gonads.

Ten modified maxillary teeth (3 specimens).

Ventrals 147–155 in males (holotype 155), 154–161 in females; subcaudals 18–21 in males (holotype 18), 14–16 in females; total length males 317–330 mm. (holotype 317), females 368–370 mm.; ratio of tail length to total length 0.072–0.106 in males (holotype 0.072), 0.073–0.076 in females.

Color of holotype brown above, yellow below, the dark pigment ending abruptly on center of third scale row; dorsal scales without network; head brown above, the dark pigment ending in an oblique line from upper edge of second supralabial to lower third of fifth; supralabials yellow, the first dark brown dorsally and anteriorly; a small yellow spot near lateral margin of parietal; head immaculate yellow below; ventrals immaculate yellow; dorsal brown color extending ventrally on tail to cover most of subcaudals, leaving a short yellow stripe along central part of each row of subcaudals.

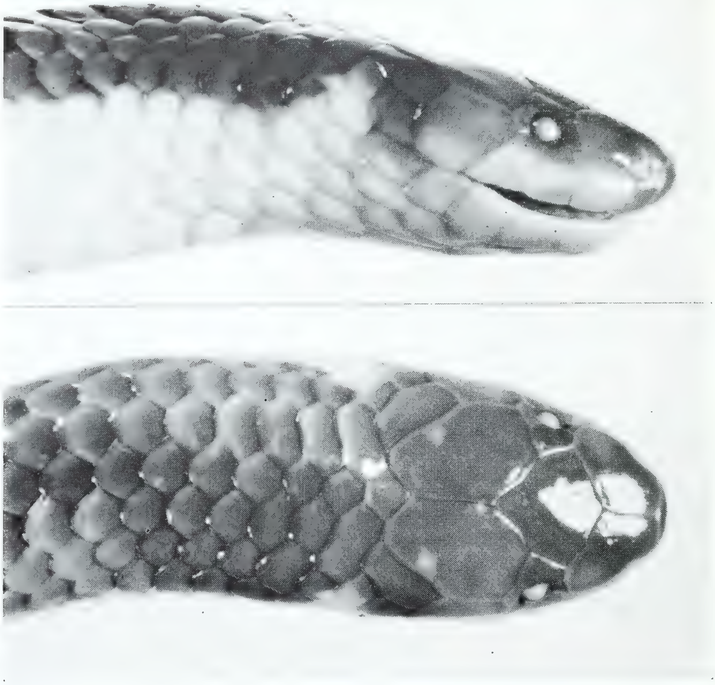

Fig. 25. Holotype of *Calamaria hilleniusi*.

Color of paratypes dark brown above, one with 21 narrow (2–3 scales wide) crossbands of lighter brown, towards rear of body crossbands become lighter; other paratypes uniformly dark brown above; dark pigment ending abruptly along second scale row; in anterior half of body first two scale rows immaculate yellow; in posterior half scales of first two rows with dark anterior edges; head dark brown above; supralabials immaculate yellow except for their dorsal edges; head immaculate yellow below; ventrals yellow, first 10 to 25 immaculate; other ventrals with dark spots at antero-lateral corners, the dark area becoming wider in posterior part of body and occupying entire width of ventrals just before vent; subcaudals yellow, edged with dark brown.

Comparisons.—*Calamaria hilleniusi* is similar to *lumbricoidea* in the relation of mental to chin shields, paraparietal and supralabial counts, and the absence of a network in the dorsal scales. It differs from *lumbricoidea* in the presence of light crossbands in some adults and the reduction of the ocular region, which is reflected in a smaller eye and wider frontal. The reduction to four dorsal scale rows takes place closer to the tip of the tail and the number of subcaudals is lower in male *hilleniusi* than in males of Borneo *lumbricoidea* (compare above description with Table 27).

Calamaria hilleniusi differs from other species related to *lumbricoidea,* e. g., *griswoldi* and *albiventer,* in coloration and in the size of the ocular region.

The patterns of *hilleniusi* are duplicated in Borneo in *C. bicolor*. *Calamaria hilleniusi* also resembles this species in its small eye and relatively wide frontal, but differs in having a laterally oriented nasal, the prefrontal separated from the third supralabial (compare Figs. 25 and 40), the mental touching the anterior chin shields, lower subcaudal counts (18–21 versus 21–28 in males; 14–16 versus 18–21 in females), and shorter tail ratios (0.072–0.106 versus 0.106–148 in males; 0.073–0.076 versus 0.079–0.093 in females).

Calamaria hilleniusi resembles *schlegeli* closely in body form, wide frontal, and small eye. The pattern of the holotype of *hilleniusi* is identical to that of *schlegeli*. *Calamaria hilleniusi* differs from *schlegeli* in having the mental touching the anterior chin shields, lower subcaudal counts (18–21 versus 27–42 in males; 14–16 versus 28 in females), smaller tail ratios (0.072–0.106 versus 0.120–0.213 in males, 0.073–0.076 versus 0.099 in females), and thicker body diameter. The holotype of *hilleniusi* is known to be sympatric with *schlegeli* at Samarinda. The specimen of *schlegeli* from Samarinda ZMA 10079) is a male with the following characteristics: 136 ventrals, 34 subcaudals, and tail ratio 0.156. The difference in ventral counts between this specimen of *schlegeli* and the holotype of *hilleniusi* suggests that the latter probably has higher ventral counts.

Distribution.—Borneo (Fig. 72).

Calamaria muelleri Boulenger. Figure 26.

Calamaria muelleri Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **17**, p. 394—Loka, Mount Bonthain, Celebes; 1897, Proc. Zool. Soc. London, **1897**, p. 223, pl. 14, fig. 1; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 86; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 161; Smith, 1927, Proc. Zool. Soc. London, **1927**, p. 224; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171; de Haas, 1950, Treubia, **20**, p. 272; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 204.

Lectotype.—Naturhistorisches Museum Basel 1690, here designated.

Taxonomic notes.—Species of *Calamaria* on Celebes fall into three morphological groups, one of which is characterized by modified maxillary teeth and relatively low ventral counts. This group of four species shows no particular specialization though two of the species, *nuchalis* and *muelleri* (Fig. 26), have narrowed snouts.

Calamaria muelleri and *C. nuchalis* are sympatric in southwestern Celebes in the vicinity of Mount Bonthain (Fig. 29). In that region the two differ in ventral coloration (immaculate in *nuchalis,* speckled in *muelleri,*) in lateral coloration (white stripe on first scale row in *nuchalis,* absent in *muelleri*), and in the number of scales and shields surrounding the paraparietal (6 in *nuchalis,* 5 in *muelleri*). These differences also distinguish these species in central Celebes where they occur though they have not been collected at the same localities.

Calamaria muelleri is apparently sympatric with *brongersmai,* the third Celebesian species having low ventral counts, in the Lake Posso area. At that place the two differ in the relative lengths of frontal and parietal shields (frontal shorter than parietal in *brongersmai,* usually longer in *muelleri*), relation of the mental and anterior chin shields (separated in *brongersmai,* touching in *muelleri,*) shape of snout (broadly rounded in *brongersmai,* narrow and with an enlarged rostral in *muelleri*), and ventral coloration (bold black squares in *brongersmai,* speckled in *muelleri*).

The fourth of these species, *boesemani,* is not sympatric with *muelleri.* The latter differs from *boesemani* in having the mental touching the chin shields and the frontal longer than the parietal and in lacking a light stripe on the first scale row.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; 5 shields and scales surrounding paraparietal; dorsal scales with a light or dark network; subcaudals 21 or less in males and 15 or less in females; portion of rostral visible from above at least equal to length of prefrontal suture; head distinctly tapered in front of eyes.

Description.—Head distinctly narrowed anteriorly; rostral as high as wide, portion visible from above equal to or longer than prefrontal suture; prefrontal ⅔ length of frontal, touching first 2 supralabials; frontal hexagonal, 1¾ to 3 times width of supraocular, equal to or longer than length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye equal to or slightly greater than eye-mouth distance; 5

supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal or second slightly larger; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.007–0.042 (10 specimens); tail gradually tapering to a moderate point; dorsal scales reduce to 4 rows on tail opposite second to eighth subcaudal anterior to terminal scute.

Hemipenis forked opposite fifth or sixth subcaudal; retractor beginning opposite seventh to ninth subcaudal, calyces smooth (4 specimens). Cloaca cardioid (1) or bulbous (1).

Nine to 11 modified maxillary teeth (8 specimens).

Ventrals: males, 129–155 (mean 146.7; N=30); females, 155–178 (mean 167.7; N=38). Subcaudals: males, 16–21 (mean 18.5; N=29); females, 9–15 (mean 12.8; N=38).

Total length: males, 116–262 mm.; females, 136–355 mm. Ratio of tail to total length: males, 0.072–0.101 (mean 0.089; N=29); females, 0.041–0.062 (mean 0.050; N=37).

Color brown above, each scale with a fine dark network; scattered scales with dark central spot; spots not forming lines; first scale row usually lighter than those above but without light longitudinal stripe; head brown, densely spotted with blackish brown; a dark stripe usually running from nasal back through eye along lower portion of prefrontal and upper margins of supralabials, descending slightly to include upper half or two-thirds of last supralabial and lower edge of parietal; remainder of supralabials yellow with a dark stripe along lower edge or with dark sutures; underside of head yellow with dark spots; ventrals highly variable but always with dark brown pigment, in the form of small spots in longitudinal rows, in the form of speckling, or as transverse bands along anterior half of each ventral; underside of tail with a broad median brown stripe and a narrower brown stripe along outer edges of subcaudals, the two stripes separated by a yellow stripe; in some specimens underside of tail dark brown with a few isolated spots.

Distribution.—Central and southwestern Celebes (Fig. 29).

CELEBES (NMS 2 unnumbered; ZMB 15638), south Celebes (BM 96.4.29.32–33): Mount Bonthain (NHMW 16691; ZSBS 545/20), Djikoro (AMNH 63381–82; BM 1926.8.20.159–166; CNHM 83162; MCZ 25315–24, 25326–33; USNM 120813), Loka (CNHM 104619; NMB 1690—lectotype, 1691–93—paratypes, 5227), Idrulaman(BM

96.4.29.27[2]), Bua Praeng (NHMW 16692: 1-10; SNG 19942-43); Luhu (BM 96.12.9.67), between Lake Posso and Gulf of Tomini (NMB 1694).

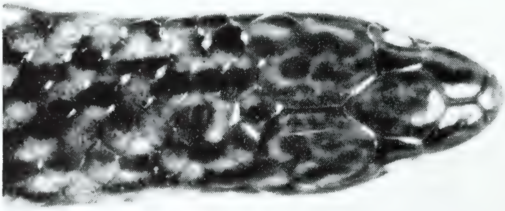

FIG. 26. Paratype of *Calamaria muelleri* (NMB 1692).

No data (BM 1946.1.1.82-84; MZUS 2 unnumbered).

?Java (ZMB 13946, 13948[3]). As these snakes were collected by the same person (Fruhstorfer) and on the same date as SNG 19942-43, they certainly must have come from Celebes.

Specimens examined.—68

Calamaria joloensis Taylor

Calamaria joloensis Taylor, 1922, Phil. Jour. Sci., **21**, p. 203—central Jolo Island, Philippine Islands; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 170; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 203; Leviton, 1963, Proc. Calif. Acad. Sci., **31**, p. 387.

Holotype.—California Academy of Sciences 60901.

Taxonomic notes.—The holotype has the lowest ventral count we have observed in the genus. The number of supralabials, eye size, position of nasal, and relation of mental and chin shields recall *hilleniusi* of Borneo. But *joloensis* differs from that species in having relatively longer parietals (equal to half of the head length), a blunter tail, fewer ventrals, and light network on each dorsal scale. Except for the much smaller eye and lower ventral count, *joloensis* is similar to *gervaisi* of the Philippine Islands.

As the unique specimen of *joloensis* is not sympatric with either *hilleniusi* or *gervaisi*, a certain decision as to the specific differentiation of *joloensis* is not possible now. However, because we have not observed intraspecific variation in eye size that could account for the difference between *gervaisi* and *joloensis*, we recognize the latter as a full species. For a similar reason, the shape of the head suggests that *joloensis* is specifically distinct from *hilleniusi*.

Diagnosis.—Maxillary teeth modified; third and fourth supralabial entering orbit; preocular present; mental touching anterior chin shields; eye about two-thirds eye-mouth distance; dorsal scales with a light network.

Description.—Rostral broader than high, portion visible from above about half length of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 3 times width of supraocular, about 3/4 length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal larger than postocular; preocular present; neither ocular as high as eye; eye $^7/_{10}$ of eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first, third, and fourth subequal and smaller than second; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.010; tail short, thick, tapering near end to a blunt tip; dorsal scales reduce to 4 rows on tail opposite sixth subcaudal anterior to terminal scute.

Hemipenis bifurcate.

Eight modified maxillary teeth.

Ventrals 119 in male; subcaudals 13; total length 144 mm.; ratio of tail length to total length 0.069.

Color faded in preservative but dark brown above, each scale with a light network; head dark brown above and on sides; head below evidently with brown spots on labials; ventrals yellowish, those in anterior part of body with dark pigment in antero-lateral corners, increasing amounts of dark pigment on ventrals farther back on body; in posterior two-thirds of body most ventrals with a dark band across anterior halves; underside of tail with dark pigment but pattern too faded for accurate observation.

Distribution.—Jolo Island, Philippine Islands (Fig. 68).

Central Jolo Island (SU 60901—holotype).

Calamaria bitorques Peters. Figure 27.

Calamaria bitorques Peters, 1872, Monatsber. Akad. Wiss. Berlin, **1872,** p. 585—Philippine Islands; Boulenger, 1894, Cat. Snakes Brit. Mus., **2,** p. 338; 1896, Cat. Snakes Brit. Mus., **3,** p. 646; Boettger, 1886, Ber. Senck. Naturf. Ges., **1886,** p. 105; Taylor, 1922, Snakes Phil. Ids., p. 185; Werner, 1929, Zool. Jahrb., (Syst.), **57,** p. 170; Marx and Inger, 1955, Fieldiana, Zool., **37,** p. 200; Leviton, 1963, Proc. Calif. Acad. Sci., **31,** p. 390.

Calamaria gervaisi (non Duméril and Bibron), Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 83 (part).

Holotype.—Zoologisches Museum Berlin 7444.

Taxonomic notes.—*C. bitorques* is very similar to *C. gervaisi* in counts and shape of head scales. The two differ in coloration and size. The former has black edged crossbands on the anterior part of the body (Fig. 27). *C. gervaisi* may have narrow yellow rings behind the head forming a wide cross band, but the band thus formed does not have dark edges. The difference in color pattern is not an effect of ontogenetic change for the characteristic pattern of *bitorques* is present in specimens in the size range 150–260 mm., which is well within the size range of *gervaisi.*

The largest *gervaisi* we have seen measured 321 mm. None of the more than 80 *gervaisi* from Luzon exceeded 290 mm. By contrast 11 of 20 *bitorques* (known from Luzon only) were longer than 300 mm., with a maximum of 420 mm.

We have examined specimens of both species from Manila, Mount Isarog (Camarines Sur), and Bulusan (Sorsogon). The size and coloration differences just noted distinguish these two species at each of these localities.

These species also differ in average number of subcaudals. Female *gervaisi* from Luzon have 10–15 subcaudals (mean 12.67, mode 13, N=78); female *bitorques* have 12–17 (mean 15.3, mode 15, N=14). Male *gervaisi* from Luzon have 15–20 subcaudals (mean 16.68, mode 16, N=65); male *bitorques* have 17–20 (mean 18.33, N=6). Female *gervaisi* from Manila have 10–14 subcaudals (30 specimens) and female *bitorques* 15–17 (2). Female *gervaisi* from Mount Isarog have 11–13 subcaudals (4 specimens) and female *bitorques* 14–15 (2). A single female of *gervaisi* from Bulusan has 16 subcaudals and a single female of *bitorques* 14. Males of both species were not available from these localities.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 5 shields and scales; 2 to 6 dark, black-edged, crossbands behind the head.

Description.—Rostral as wide as high, portion visible from above about ⅔ length of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 1½ to 2 times width of supraocular, about 5/6 length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 scales and shields; nasal much smaller than postocular; preocular present; postocular not as high as eye; eye equal to or slightly greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

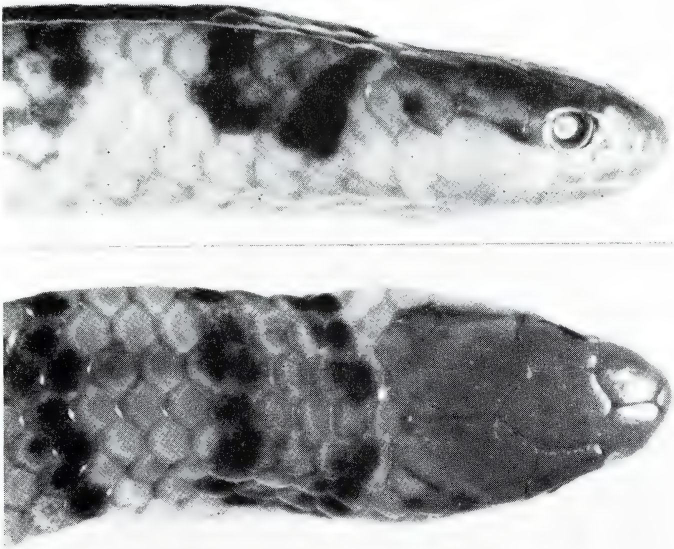

FIG. 27. Holotype of *Calamaria bitorques.*

Body thickness index 0.016–0.063 (7 specimens); tail thick, tapered near end to blunt point; dorsal scales reduce to 4 rows on tail opposite sixth to eleventh subcaudal anterior to terminal scute.

Cloaca of females bilobed (1) or cardioid (1).

Nine modified maxillary teeth (2 specimens).

Ventrals: males, 150–157 (mean 154.0; N=5); females, 157–197 (mean 173.4; N=14). Subcaudals: males, 17–20 (mean 18.3; N=6); females, 12–17 (mean 15.3; N=14).

Total length: males, 150–333 mm.; females, 222–420 mm. Ratio of tail to total length: males, 0.066–0.087 (mean 0.076; N=5); females, 0.039–0.086 (mean 0.057; N=14).

Color light to dark brown above; dorsal scales with fine dark network; 2 to 6 dark-edged saddles on anterior part of body reaching the second or third scale row; behind area of saddles dorsum usually with scattered small, dark spots; scales of first row usually immaculate yellow at least in anterior half of body; head brown above with obscure dark markings; supralabials usually cream-colored without dark spots; a dark streak extending from nasal across lower edges of prefrontal and parietal and upper edge of last labial; underside of head yellowish, usually immaculate; ventrals immaculate yellow or with dark lateral edges; underside of tail immaculate yellow or with narrow dark mid-ventral streak.

Distribution.—Luzon (Fig. 68).

LUZON (BM 72.8.20.49; ZMB 3778, 7444-holotype, listed in Berlin Museum catalogue as from "Luzon"), central Luzon (SNG 19394). Cagayan Province: Cape Engano (BM 95.9.21.4). Isabela Province (CAS 15295). Rizal Province: Manila (MHNP 00–364–65), area between Subic Bay south to Clark Air Force Base (MVZ 73672). Camarines Sur Province: Mt. Isarog, Curry, Pili (CNHM 142515–16). Sorsogon Province: Bulusan (CNHM 142510–14).

PHILIPPINE ISLANDS (BM 72.10.11.16, 72.10.11.20, 1 unnumbered; MCZ 25776).

Specimens examined.—20.

Calamaria gervaisi Duméril and Bibron. Figure 28.

Calamaria gervaisii Duméril and Bibron, 1854, Erp. Gèn., **7**, p. 76—"Java" [in error]; Günther, 1858, Cat. Colubrine Snakes Brit. Mus., p. 4; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 8; 1865, Icon. Ophid., **10**, pl. 2, fig. 1; Fischer, 1885, Jahrb. Wiss. Anst. Hamburg, **2**, p. 80; Boettger, 1886, Ber. Senck. Naturf. Ges., **2**, p. 105; 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 83; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 338; Taylor, 1922, Snakes Philippine Ids., p. 186; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 180.

Calamaria gervaisii gervaisii, Taylor, *op, cit.*, p. 187; Leviton, 1963, Proc. Calif. Acad. Sci., **31**, pp. 390, 394, 407.

Calamaria mindorensis Boulenger, 1895, Ann. Mag. Nat. Hist., (6), **16**, p. 481—Mindoro; 1896, Cat. Snakes Brit. Mus., **3**, p. 646; Taylor, *op. cit.*, p. 190; Werner, *loc. cit.*, p. 171; Marx and Inger, *loc. cit.*, p. 207.

Calamaria gervaisii iridescens Taylor, 1917, Phil. Jour. Sci., **12**, p. 360— Canlaon Volcano, Negros; 1922, *op. cit.*, p. 188; Brown and Alcala, 1961, Ecology, **42**, p. 632; Leviton, *loc. cit.*, pp. 384, 398, 402.

Calamaria tropica Taylor, 1922, Snakes Philippines Ids., p. 194—near Naujan, Mindoro; Marx and Inger, *loc. cit.*, p. 206.

Calamaria polillensis Taylor, 1923, Phil. Jour. Sci., **22**, p. 549—Polillo, Polillo Island; Werner, *loc. cit.*, p. 171; Marx and Inger, *loc. cit.*, p. 205.

Calamaria hollandi Taylor, 1923, Phil. Jour. Sci., **22**, p. 550—Port Holland, Basilan; Werner, *loc. cit.*, p. 171; Marx and Inger, *loc. cit.*, p. 202.

Calamaria gervaisi hollandi, Leviton, *loc. cit.*, pp. 379, 393.

Calamaria gervaisi polillensis, Leviton, *loc. cit.*, p. 403.

Syntypes.—Museum National d'Histoire Naturelle c2314-7202, two specimens labeled "Java". No author subsequent to Duméril and Bibron (1854) has reported this species from outside the Philippine Islands. We now believe, contrary to our previous opinion (Marx and Inger, 1955), that the type locality cannot be restricted to a particular island within the Philippines except arbitrarily.

Taxonomic notes.—We have examined the holotype of *mindorensis* Boulenger and cannot distinguish it from *gervaisi*. Boulenger (1895) did not compare *mindorensis* with any other *Calamaria*. Although our counts (ventrals 177, subcaudals 17) on the holotype differ from Boulenger's (ventrals 193, subcaudals 15) we are certain that the specimen examined is the holotype of *mindorensis* because of the agreement in coloration, size (total length 232 mm., tail length 13 mm., according to our measurements; 240 and 13 mm., according to Boulenger), and shield arrangement. Furthermore it is the only *Calamaria* from Mindoro in the collection of the British Museum.

Calamaria tropica Taylor was distinguished from all other species on the basis of the presence of loreals. These "loreals" are tiny, triangular scales much smaller than even the nasal and are wedged between prefrontal, preocular, and second supralabial. Though one of these scales appears on each side, they differ in size and we can only conclude that they represent fragments of the prefrontals. An additional specimen of *gervaisi* (SU 21804) has a similar fragment on one side of the head. The holotype of *tropica* is certainly conspecific with the other Mindoro specimens of *gervaisi* we have examined.

Calamaria polillensis was distinguished by Taylor (1923) from *gervaisi* on the basis of its lower ventral and subcaudal counts and the presence of a neck ring. As may be seen in Tables 28-31, the

TABLE 28.—Frequency Distribution of Ventral Counts in Males of *Calamaria gervaisi*.

	Class centers											
	133	*136*	*139*	*142*	*145*	*148*	*151*	*154*	*157*	*160*	*163*	Mean ± SE
Luzon (total)					1	11	11	9	3	3		151.9±0.61
Manila						10	8	6	1			
Montalban							2					
Baguio									1	2		
Lesseb										1		
Mt. Maquiling					1			1				
Mt. Arayat							1	1				
Los Banos								1				
Siniloan						1			1			
Mindoro						3		1				149.5
Polillo	1											132
Panay: Iloilo							1		1	1		156.3
Negros (total)					1	2	3	9	2	2	3	154.7±1.02
Cuernos deNegros					1		3	5				
Dumaguete								1	2	1	1	
Mt. Canlaon								1			1	
Victorias								1				
Silay								1				
Bais						2						
La Castellana										1	1	
Cebu		1			1							143
Mindanao (total)		1			1	1						142.3
Mt. Apo					1							
Masawan						1						
Mt. Malindang		1										
Basilan	1											133

TABLE 29.—Frequency Distribution of Ventral Counts in Females of *Calamaria gervaisi*.

	Class centers														
	143	*146*	*149*	*152*	*155*	*158*	*161*	*164*	*167*	*170*	*173*	*176*	*182*	*189*	Mean±SE
Luzon (total)			1		1	3	6	18	18	1	4	1		2	165.8±0.86
Manila						1	4	6	13		1			1	
Daet														1	
Montalban						1	1	5	4	1					
Baguio								3			2				
Mt. Maquiling							1								
Los Baños								1	1		1	1			
Siniloan								1							
Cordillera								1							
San Juan								1							
Corregidor						1									
Balbalan			1		1										
Mindoro								1			1	1			170.7
Polillo			1												148
Tablas						1		1							160
Panay: Iloilo									2	2		1	1		172.7
Negros (total)							1	2	3	10	2	4			170.0±0.84
Cuernos de Negros							1	2	3	5					
Dumaguete										1		1			
Mt. Canlaon											1				
Silay										1		1			
Bais										1	1	1			
Luzuriaga										1					
La Castellana										1		1			
Mindanao (total)	2	1	1		1	1									148.7
Tagum			1		1										
Mt. McKinley	2	1													
Tatayan						1									

counts of the holotype and paratype we have seen fall within the ranges of *gervaisi* from other islands; the two paratypes not examined lie within the same range of variation.

Taylor (*ibid.*) compared *C. hollandi* with *polillensis*, which we have just shown to be a synonym of *gervaisi*, but not to *gervaisi*. The character—extent of the rostral visible from above—by which Taylor distingiushed *hollandi* from *polillensis* shows considerable variation in *gervaisi*. The direct comparison of the holotype of *hollandi* to various populations of *gervaisi* does not reveal any differences of diagnostic value.

Taylor (1917) distinguished his Negros form, *C. gervaisi iridescens*, from *gervaisi* from other islands in the Philippines by ventral and subcaudal counts and by size. Marx and Inger (1955) substantiated the count differences on the basis of 17 specimens from Luzon and Mindanao. However, with larger series available these differences do not appear to be taxonomically significant (Tables 28–31).

Only the holotype of *iridescens* is unusually long (306 mm.). The largest of the 5 paratypes measured 240 mm. Of the *gervaisi* we measured, 18 of 97 from Luzon, 1 of 2 from Tablas, 4 of 8 from Panay, 1 of 9 from Mindanao, and 10 of 49 from Negros exceeded 250 mm.

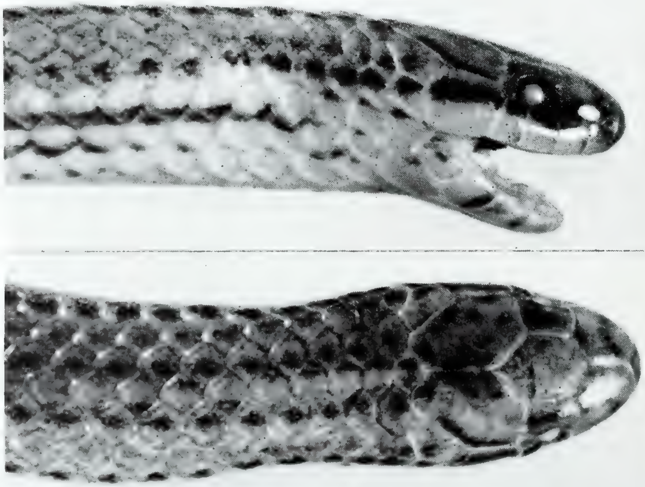

FIG. 28. *Calamaria gervaisi* (CNHM 15031).

As approximately the same proportion of the Luzon and Negros samples fall in this size range, the supposed difference between *iridescens* and other *gervaisi* has no taxonomic significance.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 5 shields and scales; subcaudals of males under 23, of females under 20; no light stripes above second scale row; a dark-edged, interrupted, light stripe on first scale row usually present; no dark-edged dorsal saddles; head not conspicuously tapered before eyes.

Description.—Rostral broader than high or higher than broad, portion visible from above $\frac{1}{3}$ to equal to prefrontal suture; prefrontal about $^4/_5$ length of frontal, touching first 2 or 3 supralabials: frontal hexagonal, $1\frac{1}{3}$ to $2\frac{1}{2}$ times width of supraocular, about $\frac{3}{4}$ to $^4/_5$ length of parietal; parietal $1\frac{1}{2}$ to $1\frac{2}{3}$ times length of prefrontal; paraparietal surrounded by 5 shields and scales (rarely 3, 4, or 6); nasal smaller than postocular; preocular present; neither ocular as high as eye; eye slightly less than or slightly greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal, or fourth narrower than others; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.007–0.030 (21 specimens); tail thick, tapering gradually to a point; dorsal scales reduce to 4 rows on tail opposite third to twelfth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth to sixth subcaudal; retractor muscle beginning opposite ninth or tenth subcaudal; sulcus bifurcate; calyces smooth (2 specimens). Cloaca of female shallowly bilobed (3) or cardioid (1).

Eight or 9 modified maxillary teeth (9 specimens).

Ventrals: males, 132–164 (mean 151.2; N=81); females, 142–190 (mean 166.1; N=101) (Tables 28 and 29). Subcaudals: males, 15–21 (mean 17.2; N=110); females, 10–18 (mean 13.2; N=129) (Tables 30 and 31).

Total length: males, 79–251 mm.; females, 104–321 mm. Ratio of tail to total length: males, 0.063–0.096 (mean 0.075; N=81); females, 0.041–0.070 (mean 0.051; N=98).

Color light or dark brown above; each scale above first row yellowish with a dark network; some scales with a dark spot forming longer or shorter dark stripes; scales of first row dark or with clear yellow centers forming a row of yellow dots; head above same color as body with irregular dark spots; lower half of supralabials yellowish, occasionally sutures dark brown; 1 or 2 complete or incomplete yellow rings on head and neck, present or absent (Table 32); underside of head yellowish, usually with small dark spots; ventrals yellowish with dark lateral edges, or yellowish with dark transverse bands across anterior halves or any condition between these two extremes (see *Geographic variation* and Table 32); underside of tail similar to belly, with or without a dark mid-ventral streak.

TABLE 30.—Frequency Distribution with Respect to Certain Characters of Males of *Calamaria gervaisi.*

Subcaudals

	15	*16*	*17*	*18*	*19*	*20*	*21*	Mean ± SE
Luzon......	4	30	19	8	3	1		16.68±0.10
Mindoro....		2	1		1			17.0
Polillo......					1			19
Panay......				2	1			18.3
Negros.....			7	9	9	1		18.15±0.17
Cebu.......				2				18
Mindanao...				1	1		1	19.3
Basilan.....			1					17

Position of reduction to four dorsal scale rows[1]

	5	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	
Luzon......		1	3	10	22	14	10	2	2	1	9.5±0.2
Mindodo....				1	2		1				9.3
Polillo......								1			12
Panay......								2	1		12.3
Negros.....					5	3	6	6	3	5	11.5±0.3
Cebu.......				1			1				9.5
Mindanao...		1	1				1				8
Basilan.....	1										5

Tail ratio[2]
Class centers

	64	*67*	*70*	*73*	*76*	*79*	*82*	*85*	*88*	*91*	*94*	*97*	
Luzon......	1	4	9	12	7	6	1	1					73±0.7
Mindoro....		1			1	1	1						76
Polillo......												1	96
Panay......			2	1									71
Negros.....		2	3	1	10	4	2	1					76±0.9
Cebu.......							1						83
Mindanao...							1	1	1				85
Basilan.....									1				88

[1] Position given in terms of subcaudals counted from vent.

[2] Ratio given in thousandths of total length.

Geographic variation.—*C. gervaisi* shows an extremely wide range of ventral counts if the entire species sample is considered, but relatively narrow ranges of variation within local samples (Tables 28 and 29). For example, the total range of ventral counts in males from Negros Island extends from 144 to 164 whereas males from Cuernos de Negros have exactly half that amount of variation. In general, the populations from the southern Philippine Islands have lower ventral counts than those from the central and northern islands. The differences between the 2 large samples, Luzon and Negros, are statistically significant though we attach no taxonomic importance to a difference of only 5 ventrals.

Subcaudal counts (Tables 30 and 31) of the northern populations are lower than those from the central and southern populations.

TABLE 31.—Frequency Distribution with Respect to Certain Characters in Females of *Calamaria gervaisi*.

Subcaudals

	10	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	Mean ± SE
Luzon	1	10	19	34	12	2				12.67±0.11
Mindoro				1				1	1	16
Polillo						1				15
Tablas				1	1					13.5
Panay				3	3					13.5
Negros		2	2	6	11	3		1		13.60±0.25
Mindanao					4		2			14.7

Position of reduction to four dorsal scale rows[1]

	3	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	
Luzon	1	5	8	23	16	8	3	4		6.3±0.2
Mindoro			1						1	8
Polillo					1					7
Tablas				1			1			7.5
Panay	1					2	2	1		11.8
Negros			2	4	8	4	9	2		7.7±0.3
Mindanao	2	2	1			1				6.8

Tail ratio[2]
Class centers

	42	*45*	*48*	*51*	*54*	*57*	*60*	*63*	*66*	*69*	
Luzon	3	10	15	12	7	1	2				49±0.6
Mindoro					1	1				1	60
Polillo										1	68
Tablas				1	1						53
Panay	2		1	1	1						48
Negros	1	5	5	6	1	4	3		1		51±1.2
Mindanao					1	1	1	1	1	1	61

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[1] Position given in terms of subcaudals counted from vent.

[2] Ratio given as thousandths of total length.

TABLE 32.—Frequency Distribution of Yellow Collars in *Calamaria gervaisi*.

	No collar	Position of single collar				Double collars Position of second collar*	
		Parietal	Scales behind parietal			Scales behind parietal	
			4	*5*	*6*	*4*	*5*
Luzon:							
Manila	97						2
Daet						1	
Montalban	14						
Baguio	2	6					
Lesseb		1					
Mt. Maquiling	4						
Mt. Arayat	2						
Los Baños	2	4					
Siniloan	4						
Cordillera							1
San Juan		1					
Corregidor	1						
Mindoro:							
Naujan				1			
Abra de Ilos			1				
"Mindoro"	5						
Polillo: Polillo			1	1			
Tablas	2						
Panay: Iloilo	9						
Negros:							
Cuernos de Negros	20		3	2			
Dumaguete	1		3	3			
Mt. Canlaon	4						
Victorias	1						
Silay	2		1				
Bais	2		2	1			
Luzuriaga	1						
La Castellana	4						
Cebu	1	1					
Mindanao:							
Tagum		3					
Mt. McKinley		3					
Mt. Apo		1					
Tatayan		1					
Masawan	1						
Basilan					1		

The differences between the Luzon and Negros samples are statistically but not taxonomically significant.

Position of the reduction to 4 dorsal scale rows is farther removed from the vent in the central populations than in the northern and southern ones. Again differences between Negros and Luzon samples are statistically but not taxonomically significant.

The ratio of tail length to total length shows no significant geographic variation (Tables 30 and 31).

As noted above, the position and number of yellow collars varies (Table 32). Almost all Mindanao specimens have a yellow ring crossing the posterior ends of the parietal scales. Most specimens from Negros have no yellow collars, but if they are present, a single one occurs 4 or 5 scales behind the parietals. Few Luzon specimens have yellow rings; those that do have either a single ring crossing the ends of the parietals or two collars, one crossing the parietal and the second 4 or 5 scales behind the parietals. As Table 32 shows, variation in this character is extremely local. For example, most of the specimens from Los Baños, Luzon, have a single yellow collar, which is found in only 2 of 99 from Manila, less than 30 miles away. Similarly, most of the specimens from Dumaguete, Negros, have yellow collars, whereas only $^1/_5$ of those from Cuernos de Negros, 10 miles away, do.

Coloration of the ventrals varies from immaculate yellow (except for lateral edges) through increasing amounts of dark spots, ending in broad dark bands crossing the anterior ½ or ⅔ of each ventral (Table 33). All gradations between these extremes may appear in a single local population, as for example, at Manila. In other samples, for instance, the small one from Baguio, Luzon, or the larger one from Cuernos de Negros, most individuals may be concentrated at one end of the scale.

The characters discussed above vary locally and independently of one another. Under these circumstances subspecies should not be recognized.

Distribution.—Philippine Islands (Fig. 68).

Luzon (BM 72.8.20.50; NHMW 16705[2]; NMB 1704–06; USNM 56345; ZMB 3746[2], 4021[3], 6272[3],7441[2]). Central Luzon (SNG 19395–98); north Luzon, Cordillera Range (CNHM 109988); north Luzon, Lesseb (NHMW 16993). Mountain Province: Balbalan (CAS 61555–56), Baguio (CNHM 100872; MCZ 25753–56; NMB 7905–06, 7908). Pampanga Province: Mount Arayat (CAS 61812–

TABLE 33.—Frequency Distribution of Ventral Patterns in *Calamaria gervaisi.*

	Immaculate	Few dark spots	Heavy spotting or narrow dark bands	Wide dark bands
Luzon (total)	32	44	44	13
Manila	20	39	30	4
Daet	1			
Montalban	4	2	6	
Baguio			1	7
Mt. Maquiling		2	1	1
Mt. Arayat			2	
Los Baños	3	1	2	
Siniloan	3			
Cordillera			1	
San Juan	1			
Balbalan			1	1
Mindoro (total)	3	1	1	
Naujan	1			
Abra de Ilos	1			
Polillo		1		1
Tablas		1	1	
Panay: Iloilo	8	1		
Negros (total)	3	3	7	38
Cuernos de Negros	1	1	2	23
Dumaguete	1		1	5
Mt. Canlaon	1	1		2
Victorios			1	
Silay		1	1	1
Bais				4
Luzuriaga				1
La Castellana			2	2
Cebu				1
Mindanao (total)	3	2	2	2
Tagum		1	2	1
Mt. McKinley	3			
Mt. Apo		1		
Masawan				1
Basilan	1			

13). Rizal Province: Manila (AMNH 63380; BM 1938.8.7.49; CAS 61746–57; CM 2468–2507, 2509–36; MCZ 20086, 25757–67, 25770; MNHP 5506, 00359–60; NHMW 16704; SU 15969; ZMH 497), San Juan (CAS 15292). Montalban (CM 2537–38; CNHM 15025–31, 15033–36; MCZ 20087). Cavite Province: Corregidor Island (USNM 71700). Laguna Province: Los Baños (CAS 61156–57; SU 7353, 7362–64), Mount Maquiling (CM 2540[2], 2542; CAS 15315–16), Siniloan (SU 15958–61). Camarines Norte Province: Daet (ZMH 4062). Camarines Sur Province: Mount Isarog, Curry, Pili CNHM 142517–21). Sorsogon Province: Bulusan (CNHM 142522).

POLILLO (CAS 62455—holotype of *polillensis;* MCZ 25775—paratype of *polillensis*).

MINDORO (BM 95.11.7.27—holotype of *mindorensis;* CAS 73766–69). Abra de Ilos, near Calapan (MCZ 37699), Naujan (CAS 62069—holotype of *tropica*).

TABLAS (MCZ 25751–52).

PANAY. Iloilo (SU 15953–57, 15962–65).

NEGROS (NMB 9514–15). South Negros (BM 77.12.13.29). Negros Occidental Province: Victorias (USNM 78118), Silay (USNM 78134–35, 80582), Mount Canlaon (CM 2626, 2633, 8807, 8809-paratypes of *iridescens*), Cabagna-an Barrio, about 16 km. E. of La Castellana (SU 19873–76). Negros Oriental Province (MCZ 17577, 46681—paratype of *iridescens*): Luzuriaga (SU 15949), Dumaguete (CNHM 57308; SU 15947–48, 15951), Batinquil Barrio, 5–6 km. W. of Dumaguete (SU 18774), Bonghong Sitio, about 10 km. W. of Dumaguete (SU 18889), 1.5 km. W. of Valencia (SU 17931), 4–5 km. W. of Valencia (SU 17929–30), 5–6 km. W. of Valencia (SU 18238, 18908), 6 km. W. of Valencia (SU 18241–42), north side of upper Maite River ravine (SU 31866), south side of Maite River, east side of Cuernos de Negros (SU 18230–37, 18239, 18770), north peak area of Cuernos de Negros (SU 18240, 21804–05, 21900), east side of Cuernos de Negros (SU 18783), Banika River area, about 5–6 kms. W. of Dumaguete (SU 18443), Bais (CNHM 61625), Mayaposi environs, about 20 km. W. of Bais (SU 18760, 18910), Ocoy River valley, about 3 km. W. of Palimpinon (SU 18776).

CEBU (SNG 19399). Antuwanga area, about 7 km. SW. of Cebu City (SU 18229).

MINDANAO. Davao Province: Tagum (CNHM 53378–80), Mount Apo, 850 meters (CNHM 53377), Mount McKinley, 915 meters (CNHM 53374–76). Cotabato Province: Tatayan (MCZ 25771). Zambaonga del Norte Province: Malindang (SU 15968), Masawan (CNHM 96620), Dapitan Peak (SU 23172), 6–10 km. SE of Buena Suerte, west side of Dapitan Peak, about 760 meters (SU 23145, 23159–60, 23162–66). Misamis Occidental Province: 10–16 km. SE of Buena Suerte, west side of Dapitan Peak, 1070–1825 meters (SU 23134–40, 23142–43, 23146, 23148–58, 23183).

BASILAN. Port Holland (CAS 60471—holotype of *hollandi*).
?Jolo (SU 15950).

PHILIPPINE ISLANDS (BM 72.10.11.17, 5 unnumbered; NHMW 16706[6], 16814[4]; UMMZ 65433[2]; ZMB 1551[2], 5461[2]).

?Java (MHNP c2314-7202[2]—syntypes. No data (CNHM 100871; SMNS 8344).

Specimens examined.—317.

Calamaria brongersmai new species.

Calamaria virgulata (non H. Boie), Boulenger, 1897, Proc. Zool. Soc. London, **1897**, p. 225 (part); Schenkel, 1901, Verh. Ges. Basel, **13**, p. 164; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 162 (part).

Holotype.—Naturhistoriska Museet Göteborg 3229, a male from Penapuan (?Pinapolan) near Luwuk and Biak, near the tip of the eastern peninsula, Celebes. Collected by Walter Kaudern in December, 1919.

Paratype.—Naturhistorisches Museum Basel 1707, a female from near Lake Posso, central Celebes.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; paraparietal surrounded by 5 shields and scales; ventrals with dark squarish spots; no light lateral stripe on any scale row; an oblique dark stripe behind eye.

Description.—Rostral wider than high, portion visible from above equals ½ length of prefrontal suture; prefrontal shorter than frontal, touching first 2 or 3 supralabials; frontal hexagonal, 2 to 2¼ times width of supraocular, about ¾ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal smaller than postocular and oriented obliquely forward; preocular present; neither ocular as high as eye; eye equal to or slightly smaller than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first, third, and fourth subequal and slightly shorter than second; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.009 (1 specimen); tail thick, tapering at tip to a compressed point; dorsal scales reduce to 4 rows on tail opposite third to fourth subcaudal anterior to terminal scute.

Eight modified maxillary teeth (2 specimens).

Ventrals 155 in male, 157 in female; subcaudals 18 in male, 11 in female. Total length of male 225 mm., of female 189 mm.; ratio of tail length to total length 0.089 in male, 0.048 in female.

Body and tail brown above, each scale with a light network; dark brown spots in center or on edges of scattered scales; some scales of first 2 rows with yellow spots, not forming continuous lateral stripe; head brown above with darker spots; an oblique dark brown stripe from eye to posterior corner of fifth supralabial; other supralabials with dark sutures; head below yellowish with brown spots on labials and chin shields; ventrals and subcaudals yellowish with scattered dark squarish spots.

Comparisons.—All Celebesian species of *Calamaria* except some *virgulata* and *boesemani* have the mental touching the chin shields and differ from *brongersmai* in this regard. In addition, *acutirostris* and *curta* are distinguished from *brongersmai* by having unmodified maxillary teeth. *Calamaria apraeocularis* has no preocular. The latter, and *virgulata* have higher ventral counts (females in excess of 179) than *brongersmai*. Besides the difference in the mental shield, *nuchalis* and *muelleri* are distinguished from *brongersmai* in having the frontal equal to or longer than the parietal and in lacking bold black squares ventrally.

Calamaria brongersmai is sympatric with *C. boesemani* in eastern Celebes (Fig. 29) where the two differ in ventral coloration (checkered in *brongersmai*, immaculate in *boesemani*), lateral coloration (white stripe absent on first scale row in *brongersmai*, present in *boesemani*), eye size (much greater than eye-mouth distance in *boesemani*, smaller in *brongersmai*), orientation of the nostrils (pointed obliquely forward in *brongersmai*, laterally in *boesemani*), and number of scales surrounding paraparietal (5 in *brongersmai*, 6 in *boesemani*).

One of the specimens (NMB 1707) of *brongersmai* was identified by Boulenger (1897) and Schenkel (1901) as *virgulata* (*non* H. Boie, equals *modesta* of this paper). It differs from *modesta* in having lower subcaudal counts and an oblique black stripe behind the eye.

The species agreeing with *brongersmai* in having the mental separated from the chin shields, 5 supralabials, a preocular, modified maxillary teeth, and the paraparietal surrounded by 5 scales are: *bicolor*, *lateralis*, *lumholtzi*, *schlegeli*, *everetti*, *modesta*, *virgulata*, and *palavanensis*. Comparisons with *virgulata*, *modesta*, and *boesemani* are made in the preceding paragraphs.

None of these species has a dark, checkered belly or a dark, oblique stripe behind the eye. In addition, *bicolor* differs from *brongersmai* in having higher subcaudal counts and a relatively longer tail. *Calamaria lateralis* and *everetti* have the reduction to four dorsal scale rows closer to the vent than does *brongersmai*. *Calamaria*

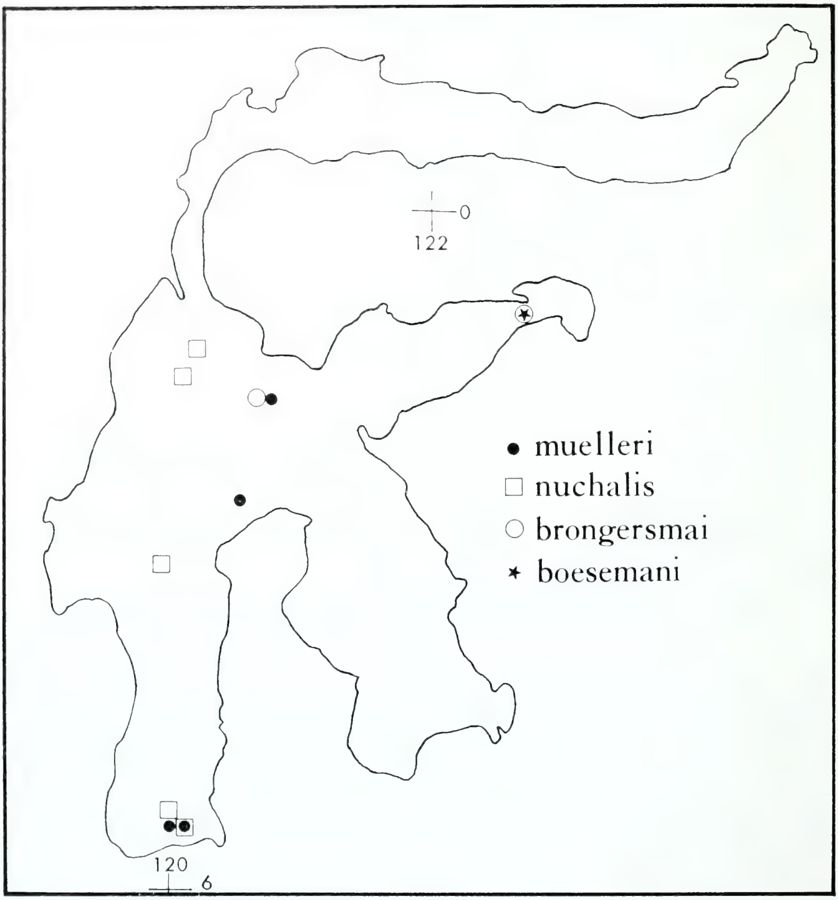

FIG. 29. Distributions of certain species of *Calamaria* from Celebes.

schlegeli and *palavanensis* have higher subcaudal counts than *brongersmai*. *Calamaria lumholtzi* differs from *brongersmai* in having a light stripe low on the side, usually no preocular, and the prefrontal as long as the frontal.

Distribution.—Central and eastern Celebes (Fig. 29).

Calamaria prakkei Lidth de Jeude.

Calamaria sumatrana (non Edeling), Sclater, 1891, Jour. Asiatic Soc. Bengal, **60**, p. 233; 1891, List Snakes Indian Mus., p. 11.

Calamaria prakkei Lidth de Jeude, 1893, Notes Leyden Mus., **15**, p. 252—Sandakan Bay, North Borneo; de Rooij, 1917, Rept. Indo-Austr. Arch.,

p. 156; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 170; de Haas, 1950, Treubia, **20**, p. 573; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 205.

Calamaria prakkii, Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 337; Bartlett, 1895, Sarawak Note Book, no. 1, p. 83.

Lectotype.—Rijksmuseum van Natuurlijke Historie 4360, a male here selected from the type series of six specimens from Sandakan Bay.

Taxonomic notes.—*Calamaria prakkei* is sympatric with *suluensis* and probably with *everetti* in eastern North Borneo. All three of these species have relatively low ventral and relatively high subcaudal counts, though *prakkei* appears to have more subcaudals. All three are alike in having a light stripe on the first scale row and a network on the dorsal scales. The mental touches the chin shields in *prakkei* and *suluensis* but not in *everetti*. The tails of *suluensis* and *everetti* taper gradually from the base whereas that of *prakkei* is thick and tapers only near the tip.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 5 shields and scales; subcaudals of males 30 or more, of females 24 or more; ventrals fewer than 145.

Description.—Rostral as wide as high, portion visible from above ½ to ⅔ length of prefrontal suture; prefrontal ¾ length of frontal, touching first 2 supralabials; frontal hexagonal, 1½ to 2⅓ times width of supraocular, about $^4/_5$ length of parietal; parietal 1⅔ times length of prefrontal; paraparietal surrounded by 5 scales and shields; nasal subequal to postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, other 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.020–0.027 (2 specimens); tail long and thick, tapering near end to sharp point; dorsal scales reduce to 4 rows on tail opposite seventh to fifteenth subcaudal anterior to terminal scute.

Hemipenis forked opposite the twelfth subcaudal, retractor beginning opposite fourteenth subcaudal; calyces papillate distally (1 specimen).

Seven to eight modified maxillary teeth (6 specimens).

Ventrals: males, 126–132 (mean 128.6; N=5); females, 142–144 (N=2). Subcaudals: males, 31–32 (mean 31.4; N=5); females, 24–25 (N=2).

Total length: males, 172–245 mm.; females, 230–256 mm. Ratio of tail to total length: males, 0.165–0.167 (mean 0.166; N=3); females, 0.096–0.105 (N=2).

Color brown above, each dorsal scale above first row with a dark network; scattered mid-dorsal scales with a dark central spot, spots not forming longitudinal stripes; scales of first row yellow in centers forming a distinct longitudinal light stripe running length of body; adjacent edges of ventrals and first scale row dark brown forming a dark stripe; a similar stripe formed along adjacent halves of first and

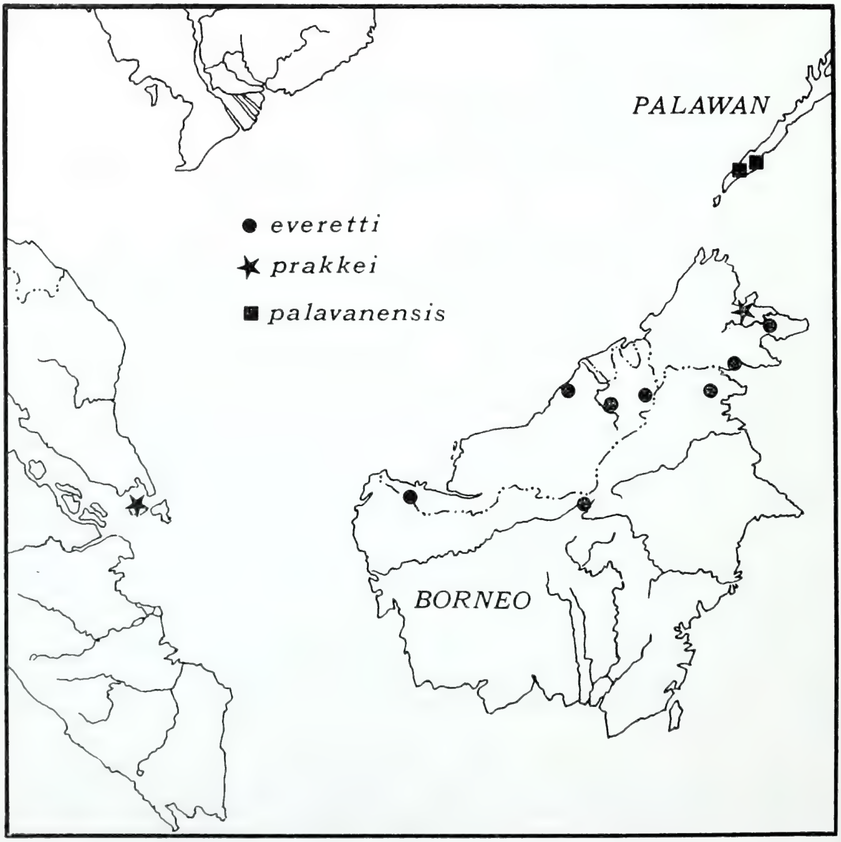

FIG. 30. Distributions of *Calamaria everetti*, *C. palavanensis*, and *C. prakkei*.

second scale rows; in anterior sixth of body a dark stripe formed on adjacent edges of second and third rows; light brown collar about 6 scales behind parietal, collar complete or interrupted mid-dorsally; head brown above with darker spots; lower half or third of supralabials yellow, sutures brown; head yellow below with brown spots on sutures; ventrals yellow, immaculate except for brown lateral edges; underside of tail yellow, usually a midventral dark stripe.

Distribution.—Northeastern Borneo and Singapore (Fig. 30).

North Borneo. Sandakan District: Sandakan Bay (RMNH 4360—lectotype, 10866[5]—paratypes).

Singapore (ZSI 13306).

Specimens examined.—7.

Calamaria suluensis Taylor. Figure 31.

Calamaria suluensis Taylor, 1922, Snakes Phil. Ids., p. 189—Cagayan Sulu, Philippine Islands; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 190; Leviton, 1963, Proc. Calif. Acad. Sci., **31**, p. 383.

Calamaria pendleburyi Smith, 1931, Bull. Raffles Mus., no. 5, p. 27—Kiau, Mount Kina Balu, North Borneo; de Haas, 1950, Treubia, **20**, p. 572; Marx and Inger, *loc. cit.*, p. 191.

Calamaria sumatrana (non Edeling),Werner, 1909, Mitt. Naturh. Mus. Hamburg, **26**, p. 228.

Calamaria grabowski (non Fischer), Marx and Inger, *loc. cit.*, p. 189 (part).

Neotype.—Chicago Natural History Museum 76294, a female from Deramakot, North Borneo; here designated.

Taylor's type of *suluensis* was destroyed in the Bureau of Science, Manila, during World War II. We know of no other specimens from Cagayan Sulu, the type locality. The neotype, collected 180 km. from the type locality is approximately the same size (neotype total

Table 34.—Comparison of Females of *Calamaria suluensis* and three topotypic C. *pendleburyi*.

Species	Locality	Ventrals	Subcaudals	Tail ratio[1]
suluensis	Cagayan Sulu[2]	154	25	102
”	Sandakan, North Borneo	168	23	92
”	Deramakot, North Borneo[3]	164	26	98
”	Bongon, North Borneo	148	25	109
pendleburyi	Mount Kina Balu	144–146	17–20	67–84

[1] In terms of thousands of total length.

[2] Holotype. Data from Taylor (1922).

[3] Neotype CNHM 76294.

287 mm., tail 28 mm.; holotype total 266, tail 27), has very similar counts (Table 34), and is the same sex.

Taxonomic notes.—We have seen two snakes from northeastern Borneo whose counts (Table 34) agree with those of the type of *Calamaria suluensis* (type locality Cagayan Sulu, Philippine Islands); they also agree with the original description of *suluensis* in other details. We are assigning these two snakes to *suluensis,* which differs from topotypic *pendleburyi* only in ventral and subcaudal counts and in relative tail length (Table 34). A female from Bongon agrees with topotypic *pendleburyi* in ventral counts and with *suluensis* in subcaudal counts and tail length. Because of this intermediate specimen and because the only differences between *pendleburyi* and *suluensis* (Table 34) involve characters known to undergo remarkable infraspecific geographic variation, we are forced to consider these two forms conspecific.

The snakes known as *suluensis* (or *pendleburyi*) and *grabowskyi* (or *baluensis*) are very similar in coloration, size of eye, shape of head shields, shape of tail, and arrangement of scales on the chin and throat. In all, the head is dark brown speckled with obscure black spots; the scales of the first row have white centers forming a continuous stripe; the ventrals vary from immaculate yellow to yellow heavily banded with dark brown. In all the frontal is relatively narrow and long, the eye is large, the nasal is almost as large as the oculars, and the mental touches the anterior chin shields. The subcaudal counts are moderate to high and the tail begins to taper almost at its base.

In the Mount Kina Balu area of North Borneo snakes were collected at Saiap, Kiau (915 meters), Kenokok (1000 meters), Tenompok (1430 meters), and Bundu Tuhan (1370 meters). The distances between localities are not great: Saiap–Kiau, 20 km.; Kiau–Kenokok, ca. 13 km., Kiau–Bundu Tuhan, 8 km.; Bundu Tuhan–Tenompok, 4 km. These distances are small enough to warrant the assumption that gene flow among populations in these localities has been likely at least up to very recent times.

The distribution in counts shown in Table 35 can be interpreted in two ways: (1) The snakes of this small area belong to one species having a remarkably wide range of variation in counts. As the two sets of counts do not overlap, one is almost forced to conclude that polymorphism is involved. As this wide, local range runs against the evidence accumulated for all the other species in the genus, this alternative lacks support.

TABLE 35.—Comparison of Counts and Tail Ratios of *Calamaria grabowskyi* and *C. suluensis* From Two Areas of Borneo.

	Map	Ventrals		Subcaudals		Tail ratio[3]	
Localities	no.[1]	G[2]	S[2]	G	S	G	S
				MALES			
Mt. Kina Balu	1	179–81(3)		28–29		94–97	
Saiap	1	180		28		93	
Kiau	1	176	131	27	20	95	104
Tenompok	1	176	136	26	18	93	79
Southeastern Borneo							
Kutei	8		133		18		88
Muara Teweh	10	150	138	23	20	100	100
Puruk Tjau	9		134		19		87
				FEMALES			
Mt. Kina Balu	1	189–90(3)		21–24		75–82	
Kenokok	1	180–88(3)		22–23		77–79	
Kiau	1		146–47(2)		17–20		67–84
Bundu Tuhan	1		144		..		..
Southeastern Borneo							
Long Petah	7	180		22		82	
Muara Teweh	10		149–61(3)		15–17		64–71
Puruk Tjau	9		158		16		74
Bandjermasin	12	190		20		69	
Telang	11	184		21		75	
Tamianglajang	11	184		20		69	

[1] Numbers in Fig. 32.

[2] G=*C. grabowskyi*, S=*C. suluensis*.

[3] Ratio in thousandths of total length.

(2) Two species differing in counts are represented.

The latter alternative is supported by differences between the two nominal forms in the relative sizes of frontal and parietal shields. In the high count group the frontal is subequal in length to the parietal, whereas in the low count group the frontal is rarely more than three-fourths the length of the parietal and is never equal to the parietal.

Although ventral coloration in the high count group varies from uniform yellow to heavy dark pigmentation (see above), the two forms differ in ventral coloration. The low count group usually has a uniformly yellow belly with a few individuals having a band of small dark spots in the midline. The high count group usually has a dark band across the anterior third or half of each ventral at least in the middle two-thirds of the body; only a few specimens have uniformly yellow ventrals or a mid-ventral band of dark spots.

The Kina Balu snakes with lower counts, parietals longer than frontals (Fig. 31), and usually immaculate yellow undersides are clearly *pendleburyi* (type locality Kiau, Mount Kina Balu), which is a synonym of *suluensis,* and those with higher counts, frontals and parietals subequal (Fig. 33), and usually dark venters are *baluensis* (type locality Mount Kina Balu), which is a synonym of *grabowskyi.*

Two groups of specimens from southeastern Borneo differ from one another in the same characters. Those with low counts (Table 35) are assigned to *suluensis* and those with high counts to *grabowskyi,* the type locality of which lies in southeastern Borneo (Fig. 32).

Calamaria everetti (type locality Senah River, western Sarawak) is very similar to *grabowskyi* and *suluensis* in the characters enumerated above, but differs in having (usually) a yellow ring around the body a short distance behind the head, a dark vertebral stripe ending on anterior half of body, and the mental separated from the anterior chin shields. The counts and tail ratio of *everetti* are similar to those of *suluensis.* The relation of mental and chin shields shows individual variation in some species (e.g., *leucogaster, modesta*) and one might consider these *everetti* as aberrant *suluensis.* But the coincident appearance of the distinctive dorsal pattern with the isolated mental shield in individuals from widely scattered localities in Borneo suggests specific differentiation.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 5 scales and shields; ventrals of males under 145, of females under 170; each dorsal scale with

TABLE 36.—Geographic Variation in *Calamaria suluensis.*

Localities	Map no.[1]	No.	Ventrals	Subcaudals	Tail ratio[2]
			MALES		
Mount Kina Balu	1	2	131–36	18–20	79–104
Bahau River	6	1	129	18	99
Kutei	8	1	131	18	88
Southeastern Borneo	9–10	2	134–38	19–20	87–100
			FEMALES		
Mount Kina Balu	1	3	144–47	17–20	67–84
Bongon	2	1	148	25	109
Eastern North Borneo	3–4	2	164–68	23–26	92–98
Sembakung	5	1	142	16	73
Southeastern Borneo	9–10	4	149–61	15–17	64–71
Sarekei	14	1	152	23	93
Cagayan Sulu	19	1	154	25	102

[1] Numbers in Fig. 32.

[2] Ratio in thousandths of total length.

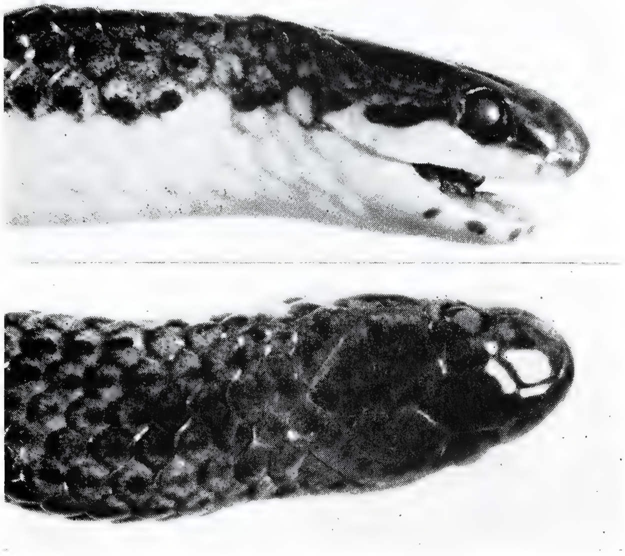

FIG. 31. Neotype of *Calamaria suluensis.*

a light network; a continuous light stripe on scales of first row only; no dark-edged saddles across anterior part of back; tail tapering gradually.

Description.—Rostral wider than high, portion visible from above about ⅔ length of prefrontal suture; prefrontal $^{4}/_{5}$ length of frontal, touching first 2 supralabials; frontal hexagonal, 1¾ to 2¼ times width of supraocular, about ¾ to almost equal to length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.009–0.028 (10 specimens); tail tapering gradually to a blunt tip; dorsal scales reduce to 4 rows on tail opposite seventh to nineteenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth or fifth subcaudal; sulcus spermaticus forked; calyces smooth (1 specimen) or papillate (1). Cloaca of female bilobed (1) or bulbous (1).

Seven to 8 modified maxillary teeth (4 specimens).

Ventrals: males, 129–138 (mean 133.5; N=6); females, 142–168 (mean 152.3; N=13). Subcaudals: males, 18–20 (mean 18.8; N=6); females, 14–26 (mean 19.0; N=12).

Total length: males, 206–241 mm.; females, 109–295 mm. Ratio of tail to total length: males, 0.079–0.104 (mean 0.093; N=6); females, 0.064–0.109 (mean 0.080; N=12).

Color brown above, each dorsal scale above first row with a fine dark network; scattered scales with dark central spots forming dashes or short lines; anteriorly first two or three scale rows white; scales of

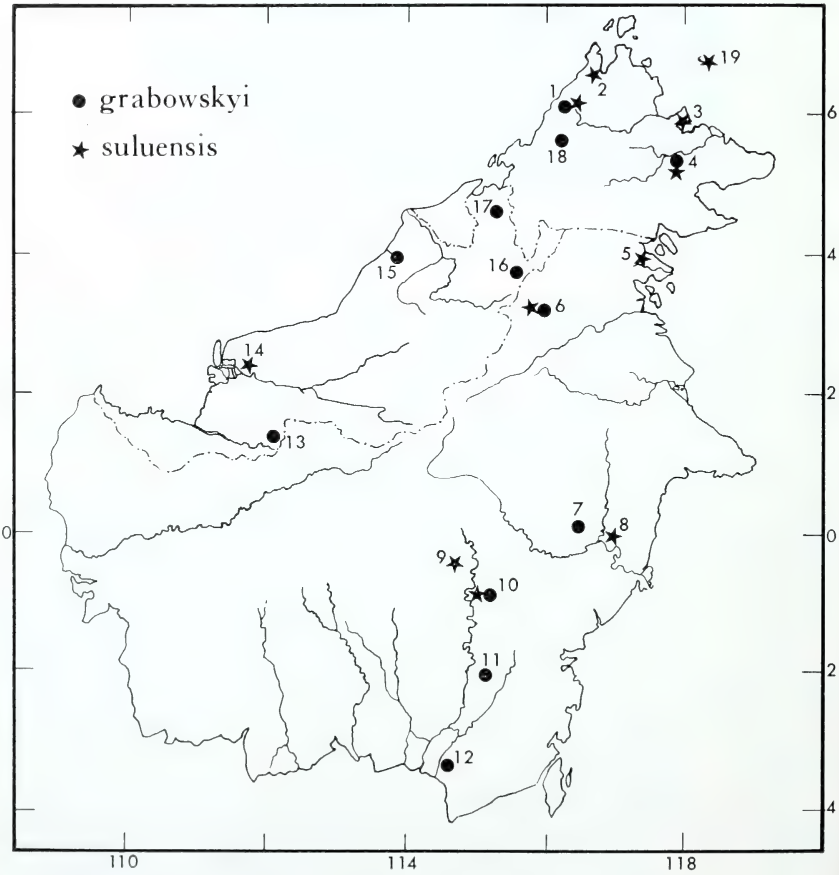

FIG. 32. Distributions of *Calamaria grabowskyi* and *C. suluensis*. Some numbered localities are listed in Tables 35 and 36. Those not in tables are: 13, Long Mujan; 15, Niah; 16, Kelabit Plateau; 17, Pa Brayong; 18, Mt. Trus Madi.

first row with light centers, forming a continuous white stripe to end of body; head dark brown above with scattered dark spots; a dark stripe along upper edges of supralabials, remainder of supralabials yellowish, with or without dark sutures; head below yellow with small dark spots on labial sutures; ventrals usually uniform yellow with dark lateral corners, some specimens with small dark spots in a broad band down center of belly; underside of tail yellow, with or without a dark median line.

Geographic variation.—The only geographic variation observed is in ventral and subcaudal counts, and in the tail ratio (see Table 36).

Distribution.—Borneo (Fig. 32) and Cagayan Sulu Island.

NORTH BORNEO. Kota Belud District: Mount Kina Balu, Kiau, 915 meters (BM 1946.1.2.12—holotype of *pendleburyi*, 1946.1.2.11—paratype of *pendleburyi;* NMS 146.17—paratype of *pendleburyi*), Tenompok, 1430 meters (NMS 18820). Ranau District: Bundu Tuhan, 1370 meters (USNM 130237), Bongon (BM 1906.5.23.5). Sandakan District: Sandakan (CNHM 63573), Deramakot (CNHM 76294—neotype).

SARAWAK. Third Division: Sarekei (CNHM 67277).

INDONESIAN BORNEO. Upper Bahau (NMHP 57812), Sembakung River (GM 3228), Puruk Tjau (RMNH 2 unnumbered), Muara Tewe (NHMW 16708[4]), Kutei (ZMH 4212); southeast Borneo (SMNS 3498).

CAGAYAN SULU (holotype destroyed at Bureau of Science at Manila; not examined).

Specimens examined.—19.

Calamaria grabowskyi Fischer. Figure 33.

Calamaria grabowskyi Fischer, 1885, Arch. Naturg. Berlin, **51**, p. 50, pl. 4, fig. 1—Telang and Tamianglajang, Dusson Timor District, Borneo; Mocquard, 1890, Nouv. Arch. Mus. Nat. Hist. Nat. Paris, (3), **2**, p. 136; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 336; Bartlett, 1895, Sarawak Note Book, no. 1, p. 83; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 155; Jong, 1928, Treubia, **10**, p. 148; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 170; Smith, 1931, Bull. Raffles Mus., no. 5, p. 28; de Haas, 1950, Treubia, **20**, p. 567; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 189 (part).

Calamaria baluensis Boulenger, 1893, Proc. Zool. Soc. London, **1893**, p. 524—Mount Kina Balu, North Borneo; 1894, Cat. Snakes Brit. Mus., **2**, p. 335, pl. 7, fig. 1; 1896, *ibid.*, **3**, p. 646; Bartlett, *loc. cit.*, p. 83; de Rooij, *op. cit.*, p. 155; Werner, *loc. cit.*, p. 170.

Calamaria moultoni Dunn, 1923, Jour. Malayan Branch Roy. Asiat. Soc., 1, p. 3—Long Mujan, Sarawak; Werner, *loc. cit.*, p. 170; de Haas, *loc. cit.*, p. 571.

Syntypes.—British Museum (Natural History) 86.5.15.13–14.

Taxonomic notes.—Smith (1931) compared the types of *moultoni*, *baluensis*, and *grabowskyi* and concluded that they belonged to a single species. We have re-examined these types and agree with Smith. Boulenger (1893) evidently did not compare *baluensis* with *grabowskyi*. One of the differences between the *baluensis* and *grabowskyi* types is the greater amount of dark pigment on the ventrals of the latter. The specimens we examined show a gradual transition from those having almost uniformly whitish ventrals to those having almost uniformly black ones.

Dunn (1923) compared *moultoni* with *indragirica* because his specimen had short black stripes anteriorly, but not with *grabowskyi* or *baluensis;* this kind of failure has been common in the history of the study of *Calamaria.*

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 5 scales and shields; reduction to 4 dorsal scale rows separated from terminal scute by 12 or more subcaudals; subcaudals 20 or more; ventrals of males 150 or more, of females usually 170 or more.

Description.—Rostral wider than high, or as high as wide, portion visible from above ½ to ¾ length of prefrontal suture; prefrontal about ¾ length of frontal, touching first 2 supralabials; frontal hexagonal, 1½ to 2 times width of supraocular, equal to length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 scales and shields (about $^1/_5$ of specimens with 4 or 6); nasal smaller than postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal, or third somewhat larger; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.011–0.062 (10 specimens); tail long, tapering gradually to a blunt tip (Fig. 10D); dorsal scales reduce to 4 rows on tail opposite twelfth to twenty-first subcaudal anterior to terminal scute; reduce to 2 rows near tip.

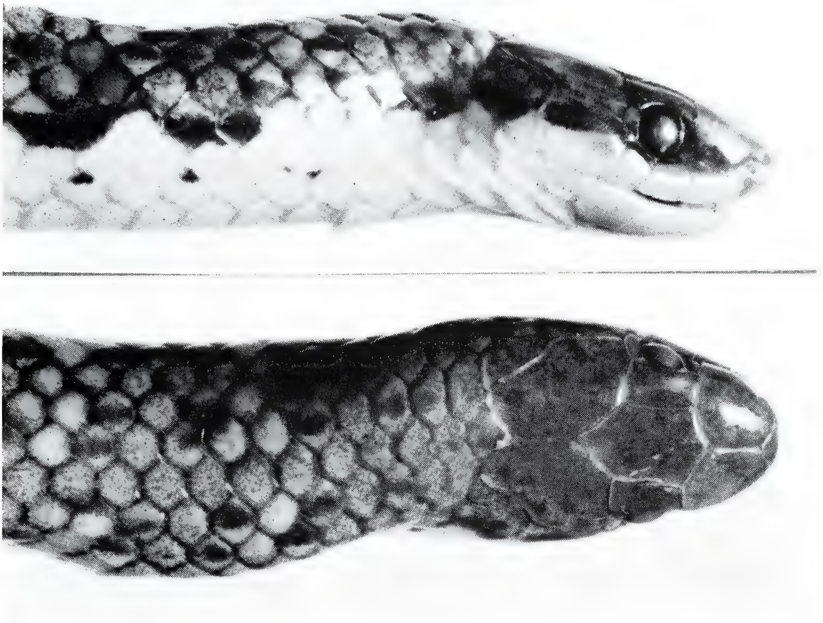

FIG. 33. *Calamaria grabowskyi* (RMNH unnumbered, "Borneo").

Hemipenis bifurcating opposite fifth subcaudal; sulcus spermaticus bifurcate, calyces smooth (1 specimen). Cloaca of female bilobed (1).

Eight to 10 modified maxillary teeth (5 specimens).

Ventrals: males, 150–186 (mean 170.7; N=15); females, 164–190 (mean 179.2; N=18). Subcaudals: males, 23–29 (mean 26.3; N=15); females, 20–28 (mean 22.6; N=18).

Total length; males, 182–365 mm.; females, 212–468 mm. Ratio of tail to total length: males, 0.085–0.104 (mean 0.095. N=15); females, 0.069–0.084 (mean 0.076; N=13).

Color dark brown above; each dorsal scale with a dark network; scattered dark brown or black spots forming dashes or short lines above; usually first three scale rows yellow just behind head, the yellow area bordered above by an irregular black stripe; scales of first row with white centers and dark edges forming a dark-edged white stripe running length of body; head brown above with dark brown or black spots; a dark brown or black stripe on side of head occupying upper third of supralabials and usually lower edge of prefrontal; lower two-thirds of supralabials yellow, with or without dark sutures; underside of head yellow, usually with small dark spots anteriorly; ventrals uniformly yellow or, more often, with varying amounts of black pigment; black pigment, when present, appears short distance behind head, taking form of median and lateral bands of transversely elongated dark spots; as amount of dark pigment increases, the rows of dark spots fuse to form a band across anterior edge of each ventral; at maximum black pigment includes all but a narrow posterior strip on each ventral; tail yellow below, with a black median band; subcaudals of some specimens with dark anterior edges.

Distribution.—Borneo (Fig. 32).

NORTH BORNEO. Kota Belud District: Mount Kina Balu (BM 93.5.30.11—holotype of *baluensis*, 95.11.7.22–23; MHNP 89191–92), Saiap (BM 96.4.29.9), Kadamayan River (MCZ 43573), Tenompok, 1430 meters (MCZ 43574), Kenokok, 1000 meters (MCZ 43570–72). Keningau District: Mount Trus Madi area (SM Cd.5.26.lg). Kinabatangan District: Deramakot (CNHM 76293).

SARAWAK. Second Division: Long Mujan (BM 1922.11.24.4—holotype of *moultoni*). Fourth Division: Niah (CNHM 129007, 131598), Kelabit Plateau (CNHM 131597; SM 6 unnumbered), Pa-Brayong (CNHM 71600).

INDONESIAN BORNEO. Bandjermasin (RMNH 568), Upper Bahau River (MHNP 57–813), Long Petah (ZMA 10230), Muara Teweh (NHMW 16998), Tamianglajang (BM 86.5.15.13—syntype), Telang (BM 86.5.13.14—syntype.)

Borneo (NHMW 16693; RMNH 3 unnumbered).

Specimens examined.—36.

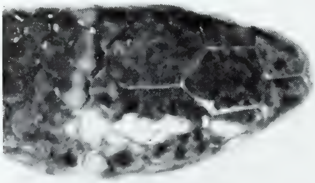

FIG. 34. *Calamaria everetti* (CNHM 131600).

Calamaria everetti Boulenger. Figure 34.

Calamaria everetti Boulenger, 1893, Proc. Zool. Soc. London, **1893**, p. 525—Sarawak; 1894, Cat. Snakes Brit. Mus., **2**, p. 340 (part); Bartlett, 1895, Sarawak Note Book, no. 1, p. 83 (part); de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 161 (part); Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171 (part); de Haas, 1950, Treubia, **20**, p. 567; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 192 (part).

Holotype.—British Museum (Natural History) 93.3.6.52.

Taxonomic notes.—Differences between *everetti* on the one hand and *grabowskyi* and *suluensis* on the other are given above (p. 126).

Several specimens from Palawan had been referred to *everetti* by various authors. These specimens are members of a distinct species, *palavanensis* (p. 134).

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; reduction to 4 dorsal scale rows separated from terminal scute by 13 or more subcaudals; eye distinctly larger than eye-mouth distance.

Description.—Rostral as wide as high, portion visible from above about ½ length of prefrontal suture; prefrontal ¾ length of frontal, touching first 2 supralabials; frontal hexagonal, 1½ to 2 times width of supraocular, about $^5/_6$ length of parietal; parietal 1½ to 1⅔ times length of prefrontal; paraparietal usually surrounded by 5 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.009–0.014 (4 specimens); tail tapering gradually to a point; dorsal scales reduce to 4 rows on tail opposite thirteenth to twenty-first subcaudal anterior to terminal scute.

Cloaca of female shallowly bilobed (1) or bulbous (1).

Nine modified maxillary teeth (3 specimens).

Ventrals: males, 140–157 (mean 148.2; N=4); females, 136–155 (mean 149.6; N=8). Subcaudals: males, 20–22 (mean 20.8; N=4); females, 16–25 (mean 20.6; N=8).

Total length: males, 96–202 mm.; females, 187–242 mm. Ratio of tail to total length: males, 0.083–0.113 (mean 0.099; N=4); females, 0.078–0.102 (mean 0.095; N=4).

Color brown above, scales with or without fine dark network; some scales with dark spots forming longitudinal lines at least anteriorly; a pale brown or yellowish vertical bar at rear of head present or absent; a similarly colored ring 6 to 8 scales behind head continuous or interrupted or absent; scales of first row with white centers forming a longitudinal stripe, usually bordered above and below by narrow dark stripes; an interrupted dark stripe formed by black spots on the fourth or fourth and fifth scale rows; a narrow dark stripe on center of vertebral row, or vertebral row pale brown flanked by a pair of narrow dark stripes, or vertebral row not distinguished from adjacent ones; stripes more conspicuous anteriorly and in smaller specimens; head brown spotted with darker brown; lower ⅔ of supralabials yellow with or without dark sutures; head below yellow, with or without dark labial sutures; belly yellow, the light color extending upward into the light rings mentioned above; lateral tips of ventrals dark brown, larger specimens with dark spots in centers of ventrals; underside of tail yellow, with or without dark midventral line.

Geographic variation.—Females from the Kelabit Plateau, Sarawak have lower subcaudal counts (16–19, 4 specimens) than do those from other parts of Sarawak (22–25, 4 specimens).

Distribution.—Western and northeastern Borneo (Fig. 30).

North Borneo. Kinabatangan District: Southeast end of Dewhurst Bay (CNHM 63572).

Sarawak. First Division: Senah branch of the Sarawak River (BM 93.3.6.52—holotype), Kuching (SM unnumbered). Fourth Division: Baram (BM 1902), Niah (CNHM 109971, 131599), Kelabit Plateau (CNHM 131600; SM 4 unnumbered).

Indonesian Borneo. Nunukan Island (GM 3227), Sembakung River (GM 3226), Mount Tibang, 1500 meters (MCZ 22649).

Specimens examined.—14.

Calamaria palavanensis new species. Figure 35.

Calamaria everetti (non Boulenger, 1893), Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 340 (part); 1894, Ann. Mag. Nat. Hist., (6), **14**, p. 84; Bartlett, 1895, Sarawak Note Book, no. 1, p. 83 (part); Griffin, 1909, Phil. Jour. Sci., **4**, p. 599; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 161 (part); Taylor, 1922, Snakes Phil. Ids., p. 191, pl. 24, figs. 5–7, text fig. 17; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171 (part); Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 192 (part); Leviton, 1963, Proc. Calif. Acad. Sci., **31**, p. 400.

Holotype.—California Academy of Sciences 62151, a male from Palawan Island, no further locality, collected by Edward H. Taylor.

Paratypes.—BM 94.6.30.50–51, 2 females from Palawan; CNHM 53381, a female from Kabelnekan, Brooke's Point, Palawan; SU 23171, a female from about 3 km. northwest of Iwahig, east slope of Thumb Peak, about 120 meters; SU 23169, a female from about 8 km. south of Bolicao, near north end of Village Range, about 60 meters.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; paraparietal surrounded by 5 shields and scales; diameter of eye longer than ventral border of prefrontal; reduction to 4 dorsal scale rows separated from terminal scute by less than 14 subcaudals; a continuous light stripe on first scale row.

Description.—Rostral broader than high, portion visible from above $2/3$ length of prefrontal suture; prefrontal $3/4$ length of frontal, touching first 2 supralabials; frontal hexagonal, $1\frac{1}{2}$ to 2 times width of supraocular, $3/4$ to $5/6$ length of parietal; parietal $1\frac{1}{2}$ to $1\frac{2}{3}$ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal large, equal to or smaller than postocular; preocular present;

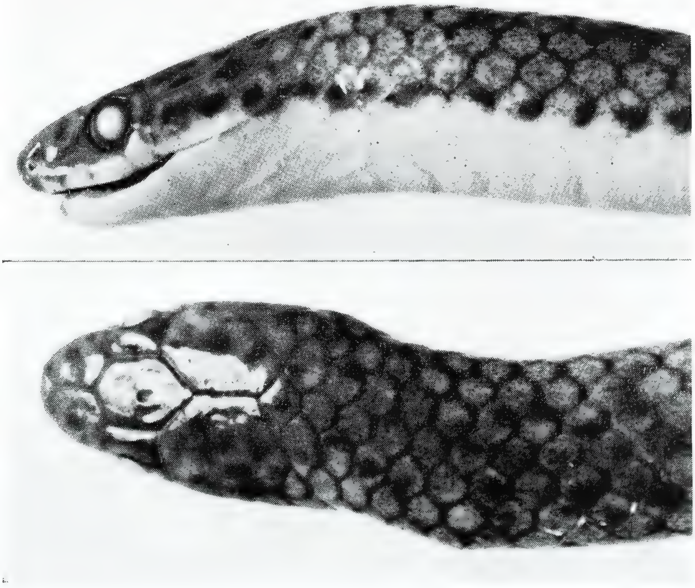

FIG. 35. Paratype of *Calamaria palavanensis* (BM 94.6.30.50).

neither ocular as high as eye; eye much greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.007–0.025 (3 specimens); tail thick, tapering near end to point; dorsal scales reduce to 4 rows on tail opposite third to thirteenth subcaudal anterior to terminal scute.

Hemipenis forked near tip; sulcus spermaticus bifurcate, calyces papillate (1 specimen).

Nine modified maxillary teeth (2 specimens).

Ventrals; males, 174–181 (mean 177.3; N=3); females, 171–187 (mean 180.2; N=5). Subcaudals; males, 23–25 (mean 24.0; N=3); females, 16–20 (mean 17.5; N=4).

Total length: males, 289–315 mm.; females, 125–323 mm. Ratio of tail to total length: males, 0.081–0.093 (mean 0.086; N=3); females, 0.055–0.067 (mean 0.061; N=4).

Color dark brown above, each dorsal scale with a fine dark network; some dorsal scales with dark central spots; spots not forming dark lines; scales of first row with light centers and dark edges forming white stripe running length of body; top of head brown with dark spots, dark pigment ending on supralabials; usually lower half of supralabials yellow, with or without dark sutures; underside of head yellow usually with dark spots on sutures; ventrals yellow, dark brown at lateral edges, central portion immaculate or with a median row of small dark spots; underside of tail yellow, with or without median dark line.

Comparisons.—Calamaria palavanensis and *virgulata* are the only species of this genus known from Palawan. These two species differ in subcaudal counts where they occur together, as south of Bolicao, Palawan. At that locality *palavanensis* has higher subcaudal counts than *virgulata* (females 16–20 compared to 8–14). The eye of *palavanensis* is much larger than that of *virgulata.* The tail of *palavanensis* tapers to a point, that of *virgulata* is blunt.

Calamaria palavanensis is most similar to *everetti, grabowskyi,* and *suluensis.* These four forms have in common similar dorsal coloration, a continuous white stripe on the first scale row, a large eye, and a moderately long tail.

Calamaria palavanensis differs from *grabowskyi* in having the mental separated from the anterior chin shields, in lacking dark cross bands on the ventrals, and in having the frontal shorter than the parietal.

Calamaria palavanensis differs from *suluensis* in having the mental separated from the anterior chin shields and higher ventral counts.

TABLE 37.—Comparison of Lengths of Certain Head Shields in *Calamaria palavanensis* and *C. modesta.*

	Lengths (mm.) of	
Species	supraocular plus prefrontal	parietal
palavanensis		
BM 94.6.30.50	3.8	3.9
CNHM 53381	3.9	3.7
CAS 62151	4.0	3.4
SU 23169	2.7	2.6
SU 23171	2.6	2.6
modesta		
SMNS 3476	3.8	4.2
SMNS 3476	3.5	3.8
SMNS 3476	4.2	5.5
SMNS 3476	4.0	4.3

Calamaria palavanensis differs from *everetti* in having a thicker and shorter tail, the reduction to four dorsal rows closer to the tip of the tail, and higher ventral counts.

The Palawan form could have been considered a subspecies of any of the three Bornean species with which we have just compared it. As these three Bornean forms are sympatric with each other they cannot be considered conspecific. The exact relationship of the Palawan form with these three cannot be determined with the material at hand. Our designation of *palavanensis* as a full species must be considered tentative.

This form is also similar to Bornean *modesta,* which have a white stripe on the first scale row. *Calamaria modesta* has a shorter snout and a slightly smaller eye than *palavanensis.* The combined length of the supraocular and prefrontal is equal to, or slightly greater than, the length of the parietal in *palavanensis* whereas this relationship is reversed in *modesta* (Table 37). The diameter of the eye in *palavanensis* is longer than the ventral border of the prefrontal; in *modesta* the diameter of the eye is sometimes equal to but usually shorter than the ventral border of the prefrontal.

Calamaria modesta shows sexual dimorphism in ventral counts (Table 39), whereas *palavanensis* does not. Only in *palavanensis* and *everetti* have we failed to find sexual dimorphism in ventral counts.

Remarks.—The two specimens formerly in the collection in the Bureau of Science, Manila, and mentioned by Taylor (1922: p. 192) are certainly this form. They were both collected at Iwahig, Palawan and their counts are incorporated into our description.

Range.—Palawan (Fig. 30).

Calamaria modesta Duméril and Bibron. Figure 36.

Calamaria modesta Duméril and Bibron, 1854, Erp. Gén., **7**, p. 74—Java; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 8; 1865, Icon. Ophid., **10**, pl. 2, fig. 5; Günther, 1873, Proc. Zool. Soc. London, **1873**, p. 168.

Calamaria monochrous Bleeker, 1860, Nat. Tijd. Ned. Indië, **21**, p. 293—Fort de Kock, Sumatra.

Calamaria bogorensis Lidth de Jeude, 1890, *in* M. Weber, Zool. Ergebn., p. 182 pl. 16, figs. 6 and 7—Buitenzorg, Java.

Calamaria modesta var. *bogorensis*, Boettger, 1894, *in* Semon, Zool. Forsch. Austr., **5**, p. 125.

Calamaria virgulata (non H. Boie), Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 340; 1896, *ibid.*, **3**, p. 647; 1897, Proc. Zool. Soc. London, **1897**, p. 225; Werner, 1896, Verh. Zool. Bot. Ges. Wien, **46**, p. 18; 1929, Zool. Jahrb., (Syst.), **57**, p. 171; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 83; Barbour, 1912, Mem. Mus. Comp. Zool., **44**, p. 120; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 162 (part); Dunn, 1927, Amer. Mus. Novit., no. 287, p. 3; Kopstein, 1930, Treubia, **12**, p. 274; 1935, *ibid.*, **15**, p. 55, pl. 1, figs. 2 and 3; 1938, Bull. Raffles Mus., no. 14, p. 132; 1941, Temminckia, **6**, p. 131; de Haas, 1950, Treubia, **20**, p. 575; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 207.

Calamaria elegans de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 158, fig. 64—Simalur Island; Werner, 1929, *loc. cit.*, p. 171; de Haas, *loc. cit.*, p. 566; Marx and Inger, *loc. cit.*, p. 201.

Calamaria simalurensis de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 159, fig. 65—Simalur Island; Werner, 1929, *loc. cit.*, p. 171; de Haas, *loc. cit.*, p. 574; Marx and Inger, *loc. cit.*, p. 206.

Calamaria lautensis (part) de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 163, fig. 66—Simalur Island; Werner, 1929, *loc. cit.*, p. 172; de Haas, *loc. cit.*, p. 569; Marx and Inger, *loc. cit.*, pp. 191, 203.

?*Calamaria mjobergi* Lönnberg and Rendahl, 1925, Ark. Zool. Stockholm, **17A**, no. 23, p. 1—Brastagi, Sumatra; Werner, 1929, *loc. cit.*, p. 172; de Haas, *loc. cit.*, p. 571; Marx and Inger, *loc. cit.*, p. 204.

Holotype.—Museum National d'Histoire Naturelle Paris 3299.

TABLE 38.—Comparison of *Calamaria modesta* and *C. virgulata.*

(Number of specimens in parentheses.)

	Ventrals		Subcaudals	
	Males	Females	Males	Females
Sumatra				
modesta	155–63(11)	171–78(7)	21–25	16–20
virgulata	. .	212(1)	. .	9
Java				
modesta	153–79(57)	165–202(49)	24–29	13–19
virgulata	189–97(3)	. .	19–22	. .
Borneo				
modesta	140(1)	152–54(3)	19	12–13
virgulata	178–83(3)	194–205(6)	18	9–16

Taxonomic notes.—We compared the holotypes of *modesta* and *virgulata,* both from Java. They differ strikingly in the shape of the tail, which tapers to a point in *modesta* but is thick and blunt in *virgulata* (Fig. 15). The holotype of *virgulata* has a pair of dorsolateral white spots opposite the vent; the posterior portion of the body and the tail of the holotype of *modesta* are uniform brown. The ventral and subcaudal counts of these two holotypes are: *virgulata* (♂) 189 and 19; *modesta* (♀) 192 and 18. Only one additional Javan specimen (USNM 44118) corresponding to the holotype of *virgulata* has been found; it is a male having 196 ventrals and 20 subcaudals. All of the numerous Javan specimens of *modesta* previously identified as *virgulata* by various authors (e.g., Boulenger, 1894; de Rooij, 1917) agree with the holotype of *modesta* and clearly differ from true *virgulata* just as does the holotype of *modesta.* Javan *modesta* have lower ventral and higher subcaudal counts than do Javan *virgulata* (Table 38).

These two species are sympatric at least on two other islands (Sumatra and Borneo) where they differ just as on Java (Table 38).

Boulenger (1894) was correct in associating *bogorensis* and *monochrous* with *modesta.*

De Rooij's *lautensis* is a composite species, being based on two specimens from Simalur Island and three from the Cocos Islands. The last three have unmodified maxillary teeth and thus differ radically from the Simalur snakes which have modified ones. We reserve the name *lautensis* for the Cocos Island population because de Rooij clearly considered the Cocos Island, Pulo si Laut, as the type locality.

De Rooij also described *simalurensis* and *elegans* from Simalur Island which makes them sympatric with Simalur "*lautensis*." These three groups (of 5 specimens) are virtually identical in ventral and subcaudal counts (Table 39), in coloration (Table 40), and in general body form, and differ only in the contact of the mental with the chin shields. In the two *lautensis* syntypes the mental is separated from the chin shields by the first infralabials. In the holotype of *elegans* the first infralabials are asymetrical, separating the mental and chin shields on one side only. In the holotype of *silamurensis* the mental meets the chin shields. The same kind of anomalies appear in the large Javan sample; of 168 specimens, 8 have the mental touching the chin shields and 7 have the asymmetrical labial pattern.

The Simalur sample is identical to our sample from Sumatra and Java except in having somewhat lower counts (Table 39), and in having white spots in the first scale row (Table 40). In these characters the Simalur snakes are identical to the Bornean sample of *modesta.*

The holotype of *mjobergi* has not been available. According to the original description, *mjobergi* differs from *modesta* only in having the eye smaller than the eye-mouth distance. In the sample we have examined the diameter of the eye is usually larger than the eye-mouth distance although it is slightly smaller in a few specimens. The holotype of *mjobergi* is the only Sumatran specimen known to have light spots in the first scale row.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; nasals oriented laterally; no light stripe occupying second and third scale rows; ventrals with dark pigment at least laterally; no oblique dark stripe behind eye; diameter of eye not longer than ventral border of prefrontal; tail tapering to a point.

Description—Rostral slightly wider than high, portion visible from above about ½ length of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 1¾ to 3 times width of supraocular, about ¾ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 or 6 shields and scales; nasal smaller than postocular; preocular present, neither ocular as high as eye; eye slightly less to slightly greater than eye-mouth distance; diameter of eye not longer than ventral border of prefrontal; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal or second slightly larger; mental tri-

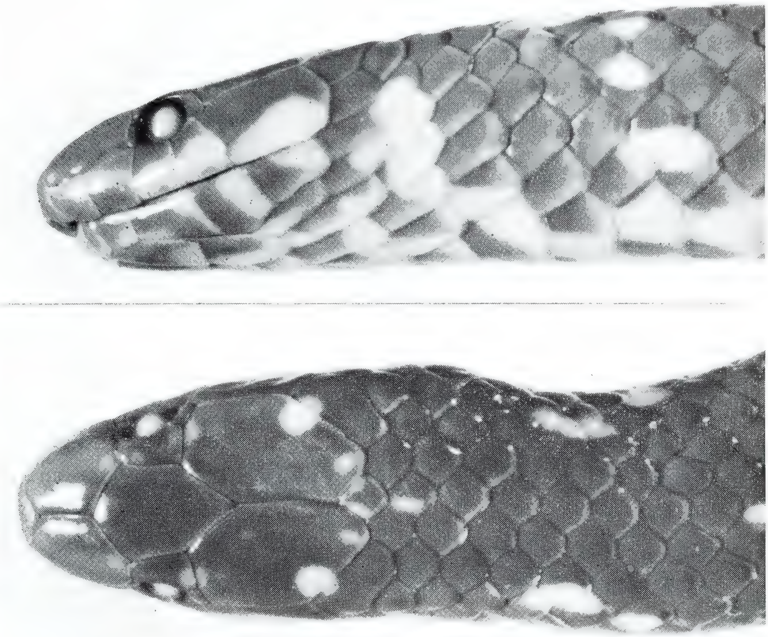

FIG. 36. *Calamaria modesta* (RMNH unnumbered, "Java").

angular, separated from anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.013–0.036 (10 specimens); tail tapering gradually to a point (Fig. 10C); dorsal scales reduce to 4 rows on tail opposite first to eleventh subcaudal anterior to terminal acute.

Hemipenis forked opposite fourth to seventh subcaudal; retractor muscle beginning opposite tenth subcaudal; calyces smooth (3 specimens).

Six to 9 modified maxillary teeth (9 specimens).

Ventrals: males, 131–179 (mean 163.0; N=97); females, 158–202 (mean 183.2; N=76). Subcaudals: males, 19–31 (mean 26.3; N=100); females, 12–21 (mean 16.8; N=79).

Total length: males, 130–411 mm.; females, 141–455 mm. Ratio of tail to total length: males, 0.088–0.155 (mean 0.109; N=90); females, 0.050–0.073 (mean 0.059; N=69).

TABLE 39.—Variation in Counts and Body Proportions of *Calamaria modesta*.

Locality	No.	Ventrals		Subcaudals		Tail ratio[1]		Reduction to four dorsals[2]	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean
MALES									
Simalur	5	131–137	133.2	25–27	26.0	131–155	141	2–7	4.2
Sumatra (Padang area)	11	155–163	159.5	21–25	23.0	93–108	100	2–5	3.3
Java: Bandung	28	165–179	172.4	25–29	27.0	91–120	104	1–7	3.0
" Tjibodas-Gedeh	18	154–166	159.9	24–28	26.1	97–116	111	1–6	3.9
" Mt. Garut	3	159–169	162.7	26–28	27.3	116–118	117	2–6	4.3
" Bogor	5	160–163	161.2	25–28	26.4	88–120	114	2–5	3.2
" Sindanglaja	2	162	..	25	..	114–117	115	3–4	3.5
" Tjisurupan	1	153	..	27	..	107	..	5	..
Borneo: Mt. Kina Balu	1	140	..	19	..	91	..	9	..
FEMALES									
Sumatra	7	171–178	174.4	16–20	18.1	60–69	66	3–10	5.6
Java: Bandung	19	191–202	195.5	15–19	17.1	50–66	56	1–4	2.5
" Tjibodas-Gedeh	25	165–194	178.1	13–18	16.2	52–65	59	1–6	2.7
" Mt. Garut	1	186	..	17	..	59	..	3	..
" Bogor	2	176–178	177.0	15–17	16.0	..	..	1–3	2.0
" Sindanglaja	1	180	..	19	..	71	..	5	..
" Tjisurupan	1	193	..	17	..	58	..	2	..
Borneo: Mt. Kina Balu	3	152–154	153.3	12–13	12.3	53–55	54	5–7	6.0

[1] Ratio in thousandths of total length.

[2] Position in terms of subcaudals from terminal scute.

Body and tail dark brown or black above; scales with a light network and an occasional dark longitudinal central streak, or scales solid brown except for a light network at edges, or scales solid black with small yellow spots scattered along body; in some specimens the dark central streaks unite to form short lines; scales of first row with or without light centers; head black above with yellow spots or yellowish brown with black spots; supralabials spotted with dark pigment; underside of head yellowish with dark spots; ventral coloration highly variable; amount of dark pigment on ventrals varies from being confined to lateral edges to covering entire width of ventrals; the light pigment confined to a narrow median strip or to a series of small semicircular spots.

Geographic variation.—The 2 largest samples from Java differ significantly in ventral counts in both sexes (Table 39). Roughly the same magnitude of difference distinguishes the Simalur and Sumatran males. The Sumatran sample (both sexes) differs from one Javan sample but not the others. The 3 Bornean females have fewer ventrals and subcaudals than those from Java and Sumatra. This species shows the same pattern of local differentiation in ventral and subcaudal counts observed in other species.

Light spots on the first scale row appear in specimens from Simalur and Borneo (Table 40).

Most of the specimens from Java and Sumatra have yellowish spots on a black or dark brown head (Table 40). In the sample from the vicinity of Tjibodas, Java, the amount of light pigment on the top of the head increases and in 8 specimens the amount of light and dark pigment is roughly equal. This last condition approaches that of the Bornean snakes, which have light brown heads with black spots.

TABLE 40.—Variation in Color in *Calamaria modesta.*

	Spots on head				White spots on first scale row	
Locality	Yellow	Y+B[1]	Black	Absent	Present	Absent
Simalur	3	0	1	1	5	0
Sumatra	17	0	0	1	0	18
Java: Bandung	49	0	0	1	0	50
Java: Tjibodas	34	8	0	0	0	42
Java: miscellaneous	11	1	0	0	0	12
Borneo	0	0	4	0	3	1

[1] Equal amounts of yellow and black.

Though the Simalur sample differs from the adjacent Sumatran series in ventrals and in lateral coloration, we do not recognize the former as a distinct subspecies as its characters are shared by the Bornean snakes. We do not view the subspecies in typological terms which would oblige one to refer the widely separated Bornean and Simalur snakes to a single subspecies split by an intervening form.

Most populations of *modesta* have 6 scales and shields surrounding the enlarged paraparietal. Of 168 specimens from Java, 4 specimens have the paraparietal surrounded by 5 scales on one side of the head and 6 on the other side; 1 specimen has the paraparietal surrounded by 7 on one side and 6 on the other. The remainder of the specimens from Java and all of those from Sumatra and Simalur have 6 scales surrounding the paraparietal. Only the specimens from Borneo have the paraparietal on both sides of the head surrounded by 5 scales.

Distribution.—Simalur, Sumatra, western Java, and Borneo (Fig. 37).

Simalur (USNM 30763): Siboga (RMNH 4715—syntype of *lautensis;* ZMA 1 unnumbered—holotype of *simalurensis*), Ayer Dingin (ZMA 1 unnumbered—holotype of *elegans*), Abail (ZMA 10112—syntype of *lautensis*).

Sumatra. Kaju Tanam (MCG 6763). Sumatera Tengah: Mount Singalong (BM 85.5.27–29, 91.11.19.24–25; MCG 6763 [8]). Ajer Manteior (MCG 6763). Sumatera Selatan: Padang (NHMW 16458, 16462[2]).

Java (BM 73.5.3.30[2]; MHNP 3299—holotype; MZUS 1 unnumbered; NHMW 16456, 4 unnumbered; UMMZ 67196; ZMB 13029[2] 24573, 29705; ZSBS 1934/0, 1935/0[2], 2646/0[3], 2675/0[2]). Djawa Barat: Bogor (CNHM 100099, 109947—syntype of *bogorensis;* MCZ 20970—syntype of *bogorensis;* RMNH 4326—syntype of *bogorensis*, 2 unnumbered; ZMA 2 unnumbered—syntypes of *bogorensis*), near Bogor (BM 98.12.30.3), Gunong Tjikuraj (NMS 2 unnumbered), Bandung (NHMW 16460[2], 16464[11]), Bandung, Rantjabali, ±1700 meters (RMNH 8603[6], 8764[6], 8771[3], 8788[4], 8953[6], 9037[10]), Bandung, Patoehawati, ±1800 meters (RMNH 10484), Bandung, Malabar, ±1600 meters (RMNH 8536), Pengalengan (MZUS 4 unnumbered; NHMW 16461; NMS 2 unnumbered; SMNS 3476[4], 3477[6]; SNG 19401–03; SU 8524), Tjiniroean, near Pengalengan (RMNH unnumbered), Sindanglaja (CNHM 83164; MCZ 7525[2]),

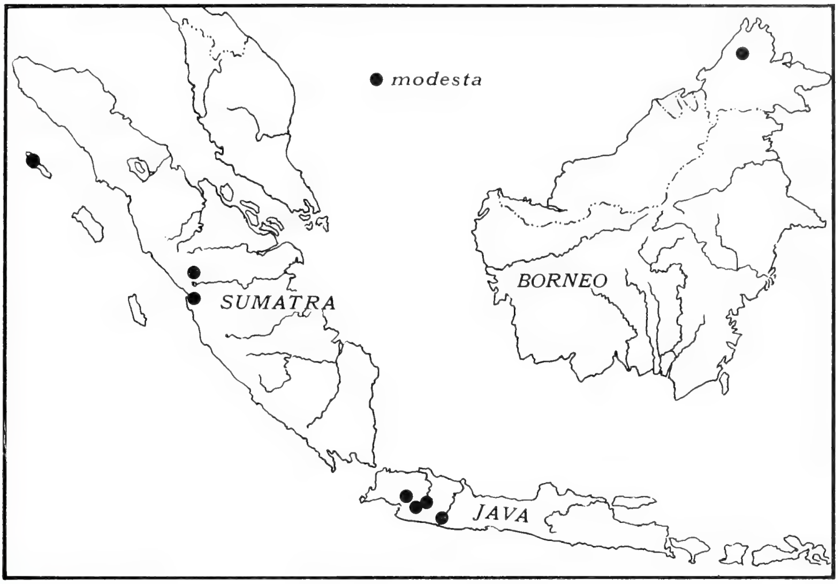

FIG. 37. Distribution of *Calamaria modesta*.

Rarahan (BM 85.5.27.22–26; MCG 6764[10]; ZMB 10264[5], 10266 [4]), Gunong Gede (NHMW 16459[5], 19463[3]), Tjibodas (AMNH 31944; MCZ 45281; RMNH 8550, 8581[2], 10485[3]; SNG 19406–07; USNM 44069, 44073; ZMB 29533), Gunong Garut (NHMW 16457; RMNH unnumbered), Gunong Garut, Kamodjang (RMNH unnumbered), near Gunong Garut, 915 meters (BM 1929.9.13.3), Tjisurupan (SNG 19404–05), Preanger District, Giriawas, 1400 meters (RMNH 10417[5], Preanger District, Gunong Manglajang (ZMA 10109) Tjikadjang, 900 meters (RMNH 10412[2]). Djawa Tengah: Wonosobo, ±1000 meters (RMNH unnumbered).

NORTH BORNEO. Kota Belud District; Mount Kina Balu, Tenompok, 1430 meters (BM 1929.12.22.113; NMS 295, 18951). Ranau District: Bundu Tuhan, 1370 meters (USNM 130236).

No data (NMS unnumbered).

?Celebes: Manado (BM 71.7.20.210–212). We reject this locality for *modesta* (Boulenger, 1894) for the same reasons given under *linnaei* (p. 207).

Specimens examined.—199.

Calamaria lateralis Mocquard. Figure 38.

Calamaria lateralis Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat. Paris, (3), **2**, p. 136, pl. 8, fig. 4—Mount Kina Balu, Borneo; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 342; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 168; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 172; de Haas, 1950, Treubia, **20**, p. 569; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 203.

Holotype—Museum National d'Histoire Naturelle Paris C231789. 194.

Diagnosis.—Maxillary teeth modified; third and fourth supralabial entering orbit; preocular present; mental not touching anterior chin shields; body color dorsally and ventrally dark brown with a continuous lateral white stripe on second and third scale rows for entire length of body and tail.

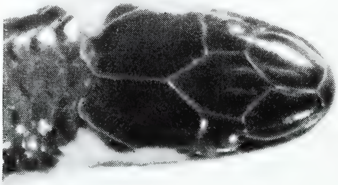

FIG. 38. *Calamaria lateralis* (MCZ 43582).

Description.—Rostral wider than high, portion visible from above equal to half length of prefrontal suture; prefrontal slightly shorter than frontal, touching first 2 supralabials; frontal hexagonal, $1\frac{3}{4}$ to $2^1/_6$ times width of supraocular, about $\frac{3}{4}$ length of parietal; parietal $1\frac{1}{2}$ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye less than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, other 4 subequal or second slightly larger than others; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.011 (1 specimen); tail tapering gradually from end of body to a point; dorsal scales reduce to 4 rows on tail opposite twelfth to sixteenth subcaudal anterior to terminal scute.

Eight modified maxillary teeth (3 specimens).

Ventrals: male, 146; females, 150–151 (N=2). Subcaudals: male, 23; females, 16–18.

Total length: male, 243 mm.; females, 190–290 mm. Ratio of tail to total length: male, 0.091; females, 0.062–0.074.

Color above and below dark blackish brown with a longitudinal white line beginning behind eye and running entire length of body in second and third scale rows.

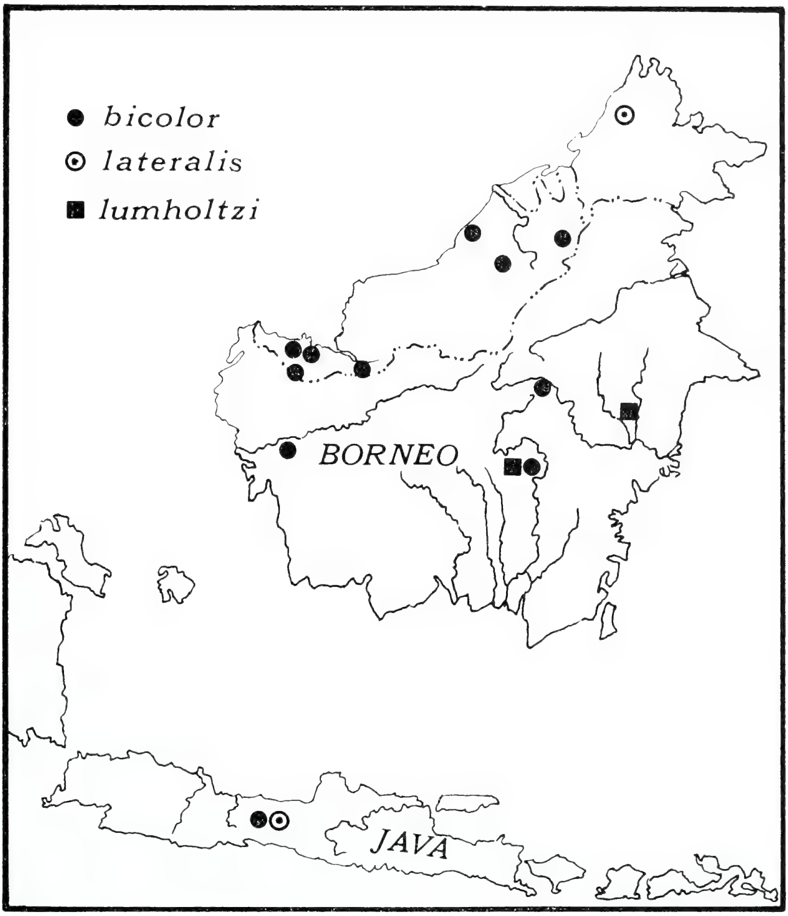

FIG. 39. Distributions of *Calamaria bicolor*, *C. lateralis*, and *C. lumholtzi*. No precise localities in Java.

Distribution.—Java and northeastern Borneo (Fig. 39).

JAVA (ZMB 29700).

NORTH BORNEO. Mount Kina Balu (MHNP C231789.194—holotype; MCZ 43582).

Calamaria lumholtzi Andersson.

Calamaria lumholtzii Andersson, 1923, Nyt. Mag. Naturk. Kristiania, **61**, p. 123—Tumbang Maruwei, Borneo; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173; de Haas, 1950, Treubia, **20**, p. 570; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 203.

Calamaria raveni Cochran, 1923, Proc. Biol. Soc. Washington, **36**, p. 92—Sungai Merah, Borneo; de Haas, *loc. cit.*, p. 573; Marx and Inger, *loc. cit.*, p. 205.

Syntypes.—Universitets Zoologiske Museum, Oslo, unnumbered, 2 females.

Taxonomic notes.—The holotype of *raveni* differs from the syntypes of *lumholtzi* only in the presence of a small preocular. Both sets of types have the same unusual coloration, which we have not seen in any other species of this genus. These two lots, both from east-central Borneo, agree also in scutellation and body proportions.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; mental not touching anterior chin shields; dorsal scales dark, a light stripe on second and third rows, bordered below by a dark stripe; ventrals white.

Description.—Rostral broader than high, portion visible from above less than half length of prefrontal suture; prefrontal equal to length of frontal, touching first 3 supralabials; frontal hexagonal, 2 to 2⅔ times width of supraoculars, about ⅔ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal smaller than postocular; preocular present or absent; postocular not as high as eye; eye smaller than eye-mouth distance; 5 supralabials, third and fourth entering orbit; fifth the largest, first and third slightly larger than second and fourth; mental triangular, separated from anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 or 4 gulars in midline between posterior chin shields and first ventral.

Tail moderately thick, tapered in posterior fourth to a blunt tip; dorsal scales reduce to 4 rows on tail opposite sixth to eighth subcaudal anterior to terminal scute.

Eight modified maxillary teeth (1 specimen).

Ventrals: females, 167–171 (mean 168.3; N=3). Subcaudals: females, 13–15 (mean 13.7).

Total length: females, 100–213 mm. Ratio of tail to total length: females, 0.053–0.056 (mean 0.055).

Color above dark brown with a longitudinal light stripe on second and third scale rows, bordered below by a dark stripe on the lower half of second and all of first scale rows; some scales in first row with light centers; head with a dark spot on adjacent quadrants of prefrontals and frontal; rest of head, above and below, light or with a dark brown spot in front of and below eye; tail light above and below with a dark longitudinal band on each side separated from dark coloration of body by a broad light area; ventrals white, sometimes with dark speckling along anterior margins.

Distribution.—Central Borneo (Fig. 39).

INDONESIAN BORNEO. Tumbang Maruwei (UZMO 2 syntypes unnumbered), Sungai Merah (USNM 51638—holotype of *raveni*).

Calamaria bicolor Duméril and Bibron. Figure 40.

Calamaria bicolor Duméril and Bibron, 1854, Erp. Gén., **7**, p. 78—Borneo; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 9; 1865, Icon. Ophid., **10**, pl. 2, fig. 6; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 342; Bartlett, 1895, Sarawak Note Book, no. 1, p. 84; de Rooij, 1917, Rept. Indo-Austr. Arch. **2**, p. 165; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 172; de Haas, 1950, Treubia, **20**, p. 564; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 200.

Calamaria macrurus Bleeker, 1860, Nat. Tijd. Ned. Indië, **21**, p. 294—Java.

Calamaria leucocephala (non Duméril and Bibron), Boulenger, *loc. cit.*, p. 344 (part).

Calamaria hosei Günther, 1896, Ann. Mag. Nat. Hist., (6), **17**, p. 229—Entoyut River, Sarawak; de Rooij, *op. cit.*, p. 178; de Haas, *loc. cit.*, p. 568; Marx and Inger, *loc. cit.*, p. 202.

Calamaria semiannulata Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 84—Borneo; Boulenger, 1899, Zool. Rec., **36**, Rept., p. 22; de Rooij, *op. cit.*, p. 172; Smith, 1925, Sarawak Mus. Jour., **3**, p. 19; Werner, *loc. cit.*, p. 173; de Haas, *loc. cit.*, p. 573; Marx and Inger, *loc. cit.*, p. 205.

Calamaria picteti Peracca, 1899, Rev. Suisse Zool., **7**, p. 325, pl. 14, figs. 1–3—Sarawak; de Rooij, *op cit.*, p. 170; Werner, *loc. cit.*, p. 173.

Holotype.—Rijksmuseum van Natuurlijke Historie 68.

Taxonomic notes.—The holotype of *macrurus* is identical to that of *bicolor*. Of special significance is the fact that *macrurus* has nasals oriented forward and smaller than the eye. In these characteristics *bicolor* differs from *schlegeli.* Boulenger (1894) was in error in placing *macrurus* in the synonymy of *leucocephala* (=*schlegeli*).

After examining the holotypes of *semiannulata* and *picteti*, we agree with Smith's decision (1925) that they are conspecific, despite the difference in the sizes of their eyes (Table 41). These two juvenile snakes have narrow rostrals, the nasals oriented forward, and their prefrontals touching the first three supralabials. These are the diagnostic characters of *bicolor*.

The holotypes of *picteti* and *semiannulata* differ strikingly from that of *bicolor* in having a dorsal pattern of dark crossbands on a light ground color. However, some adult *bicolor* have clear indications of a banded pattern. For example, two specimens (RMNH unnumbered, total length 311 mm.; and CNHM 131595, total length 331 mm.) have distinct black crossbands on a dark brown ground color; on the tail the ground color is pale yellowish brown.

The holotype of *hosei* differs from adult *bicolor* in having light intervals between the dark dorsal bands on the body. However, Günther (1896) noted that many of the scales in the light interspaces were "bordered and speckled with blackish." The coloration of the holotype of *hosei* is clearly intermediate between those of *semiannulata* and *picteti* on the one hand and the two adults mentioned in the preceding paragraph. Günther stated that *hosei* had two oblique dark bands on the side of the head; similar bands are evident on the sides of the heads of *semiannulata*, *picteti*, and the two adults.

The holotype of *hosei* differs from most specimens of *bicolor* in having the mental touching the chin shield. In one snake from Nanga Padang (NHMW 16997:2) the first infralabials meet narrowly, barely separating the mental from the anterior chin shields.

We see no reason for maintaining *hosei* as a species distinct from *bicolor*.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; paraparietals surrounded by 5 scales and shields; prefrontal touching third supralabial; no dark squares on ventrals; nasals oriented forward.

Description.—Rostral higher than wide, portion visible from above equals ½ length of prefrontal suture; prefrontal subequal to frontal, usually touching first 3 supralabials (19 of 21 specimens); frontal hexagonal, 2½ to 4 times width of supraocular, about ⅔ to ¾ length of parietal; parietal 1½ times length of prefrontal; para-

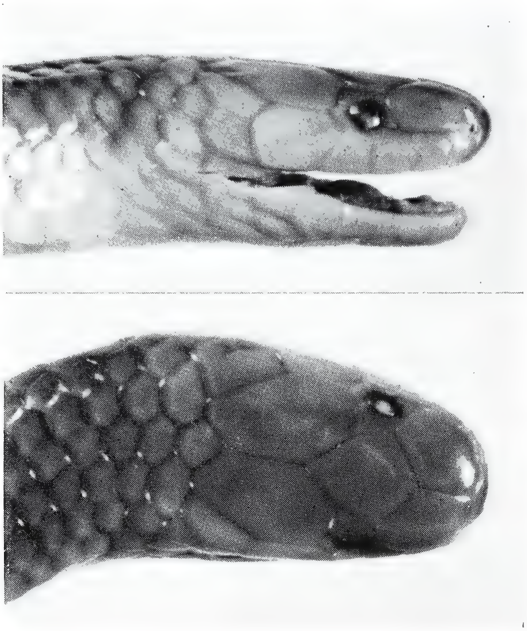

FIG. 40. Holotype of *Calamaria bicolor*.

parietal surrounded by 5 shields and scales; nasal equal to or smaller than postocular, oriented forward; vertical axis of the nostril bisected by the forward extension of the frontal-supraocular suture; preocular present, neither ocular as high as eye; eye less than eye-mouth distance (Table 41); 5 supralabials, third and fourth entering orbit, fifth the largest, first smallest, other 3 subequal; mental triangular, not touching anterior chin shields (except 1); 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.012–0.054 (8 specimens); tail thick, tapering slightly from base, abruptly near end to a blunt point; dorsal scales reduce to 4 rows on tail opposite fifth to fourteenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth to sixth subcaudal; retractor muscle beginning opposite eighth or ninth subcaudal; calyces smooth (2 specimens) or papillate (1). Cloaca of female bulbous (1) or cardioid (1).

Eight to 10 modified maxillary teeth (7 specimens).

TABLE 41.—Individual Variation in *Calamaria bicolor*.

	Sex	Total length (mm.)	Eye-mouth distance[1]	Eye diameter[1]	Ratio[2]	Dorsal pattern	No. of bands	
							Body	Tail
SM 2	♂	164	35	15	.43	banded, light interspaces	24	4
NHMW 16997:2	♂	178	32	20	.63	” ” ”	17	3
MHNG 748.36	♀	181	30	25	.83	” ” ”	30	5
SNG 19413	♂	200	. .	. .	. .	” ” ”	20	5
RMNH 68	♂	281	35	25	.71	uniformly dark	0	0
RMNH 1678	♂	284	40	25	.63	” ”	0	0
RMNH ——	♂	311	42	35	.83	banded, dark interspaces	22	5
CNHM 131595	♀	331	36	30	.83	” ” ”	18	3
RMNH 10542	♀	335	40	32	.80	” ” ”	?	4
holotype *hosei*	. .	358	. .	. .	. .	” light interspaces	18	3
SM Cd.5.26.7a	♀	391	40	30	.75	uniformly dark	0	0
CNHM 131596	♀	432[3]	60	41	.68	” ”	0	0

[1] Ocular micrometer units.

Ratio of eye diameter to eye-mouth distance.

[3] Body length, tail incomplete.

Ventrals: males, 139–169 (mean 150.3; N=12); females, 149–161 (mean 156.5; N=8). Subcaudals: males, 21–28 (mean 24.9; N=12); females, 18–21 (mean 19.4; N=7).

Total length: males, 164–450 mm.; females, 181–415 mm. Ratio of tail to total length: males, 0.093–0.148 (mean 0.115; N=12); females, 0.072–0.093 (mean 0.083; N=7).

Color of adults uniform dark brown above or with obscure black crossbands superimposed on ground color; dark pigment usually ending abruptly on second or third scale rows; scales of first and second rows sometimes with black anterior corners, forming a continuous black stripe in some specimens; head dark brown above, with or without two oblique dark bands crossing yellow lip; ventrals yellow, immaculate, rarely (3/20) spotted with black; tail above immaculate dark brown or pale brown with dark crossbands; underside of tail yellow, with or without median dark line.

Ontogenetic variation.—The four juveniles (200 mm. or less) examined have a yellow ground color with dark crossbands. The light intervals vary from 3 to 6 scales wide (modal value, 4 scales), and are as wide or wider than the crossbands. Only two adults are known to retain this pattern (Table 41). The changes in pattern associated with increased size in the limited sample at our disposal suggest ontogenetic change in color pattern.

Geographic variation.—The two males from Java have higher ventral counts (164–169) than 9 of 10 from Borneo (139–152, 167).

Distribution.—Java and Borneo (Fig. 39).

JAVA (BM 63.12.4.12—holotype of *macrurus;* ZMB 4477).

INDONESIAN BORNEO. Kapuas (RMNH 10468), Upper Mahakam (RMNH unnumbered), Muara Teweh (NHMW 16997:1), Tajan (USNM 36282), Nanga Padang (NHMW 16997:2), west coast of Borneo (RMNH 10542), southeast Borneo (RMNH 1678).

SARAWAK (BM 94.1.19.9; MHNG 748.36—holotype of *picteti*). First Division: Matang (BM 73.4.25.11), Paku, near Bau (SM Cd. 5.2.26.7a), Kuching (SM unnumbered=M. A. Smith No. 7986), Tapuh Kedup (SM unnumbered). Fourth Division: Entoyut River (holotype of *hosei*—not examined), Niah (CNHM 131595), Kelabit Plateau (CNHM 131596).

BORNEO (RMNH 68—holotype, 1442; SNG 19413—holotype of *semiannulata;* ZMB 4962).

Specimens examined.—21.

Calamaria schlegeli Duméril and Bibron.

Calamaria schlegeli Duméril and Bibron, 1854, Erp. Gén., **7**, p. 81—Borneo.

Calamaria leucocephala Duméril and Bibron, *ibid.*, p. 83—locality unknown.

Calamaria agamensis Bleeker, 1860, Nat. Tijd. Ned. Indië, **21**, p. 295—Fort de Kock, Sumatra and Singkawang, Borneo.

Keiometopon booliati Taylor, 1962, Univ. Kansas Sci. Bull., **43**, p. 258, figs. 16–17—Fraser's Hill, Malaya.

Taxonomic notes.—*Calamaria schlegeli* and *C. leucocephala* were recognized as distinct species by Duméril and Bibron and subsequent reviewers (Boulenger, 1894; de Rooij, 1917) on the basis of differences in the preocular, mental position, and color of head. After examining the holotype of *schlegeli* and numerous specimens of *leucocephala,* we find that the supposed differences in the preocular and head coloration fall into the category of individual variation.

The mental of the holotype of *schlegeli* touches the anterior chin shields. In this respect it differs from all other specimens, which have the infralabials separating the mental from the chin shields. One additional specimen (MCZ 43583), also from Borneo, has the first pair of infralabials unequally developed so that one does not separate the mental from the anterior chin shield on that side. Except for this character the holotype of *schlegeli* has all of the diagnostic characters of *leucocephala.*

Mertens (1929) and Smith (1930) pointed out that the presence or absence of the preocular could not be used to distinguish *agamensis* Bleeker from *leucocephala.* As is shown in Table 42, a preocular may be present on both sides of the head, present on one side only, or absent on both sides in Sumatran specimens.

One of the syntypes (RMNH 42) of *C. lumbricoidea* Boie is a typical Javanese *schlegeli;* its catalogue number has been changed to RMNH 10425.

The holotype and only specimen of *Keiometopon booliati* is a *schlegeli* with abnormal dorsal head shields (see p. 8). It has the large nasal characteristic of *schlegeli* and its counts (Taylor, 1962) fall within the range of variation of *schlegeli* from Malaya.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; mental not touching anterior chin shields; distinctly bicolored; dark dorsal pigment ending abruptly above first scale row, ventrals and first scale row without dark pigment; nasals oriented laterally.

Description.—Rostral broader than high, portion visible from above ½ length of prefrontal suture; prefrontal slightly shorter than frontal, touching first 2 or 3 supralabials; frontal hexagonal, 3½ to 5 times width of supraocular, about ¾ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 or 6 shields and scales; nasal larger than postocular, as large as eye; preocular present or absent; postocular not as high as eye; eye smaller than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal or first and second larger than third and fourth; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline or second pair separated; 3 or 4 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.012–0.028 (9 specimens); tail long, tapering throughout length to slightly blunt point (Fig. 14B); dorsal scales reduce to 4 rows on tail opposite third to twenty-fifth subcaudal anterior to terminal scute.

Hemipenis forked opposite third (1 specimen), fourth (11), fifth (7), or sixth (1) subcaudal; retractor muscle beginning opposite eighth (4), ninth (6), tenth (3), or eleventh (1) subcaudal; calyces smooth (6 specimens from Sumatra, 6 from Java, 4 from Borneo, 4 from Malaya).

Nine or 10 modified maxillary teeth (22 specimens).

Ventrals: males, 129–161 (mean 144.2; N=102); females, 136–180 (mean 162.8; N=115). Subcaudals: males, 25–44 (mean 32.1; N=99) females, 19–37 (mean 25.5; N=113).

Total length: males, 125–391 mm.; females, 145–395 mm. Ratio of tail to total length: males, 0.111–0.213 (mean 0.143; N=97); females, 0.073–0.144 (mean 0.101; N=111).

Color dark above, light below; scales above first or second rows without network, dark brown or black; head yellow above and below or black above and yellow below, or various intermediate conditions (see below); ventrals and first one or two scale rows immaculate yellow.

Geographic variation.—A preocular is present in all snakes from Singapore and Malaya; it is virtually absent in the Javan sample, and intermediate in frequency in the Bornean and Sumatran samples (Table 42). When present the preocular varies in size and shape from a vertically elongated rectangle reaching the supraocular to a small triangular or horizontally elliptical scale widely separated from the supraocular. The prefrontal scale is separated from the eye when the preocular is large, but touches the eye when the preocular is

Table 42.—Frequency Distribution of Preocular Counts Within Various Samples of *Calamaria schlegeli*.

	Preocular counts		
	1/1	*1/0*	*0/0*
Northern Malaya	11	0	0
Central Malaya	3	0	0
Singapore	10	0	0
Northern Sumatra (Deli)	2	0	0
Northern Sumatra (Tawar)	3	0	2
Western Sumatra	6	1	10
Southeastern Sumatra	4	1	0
"Sumatra"	1	0	0
Bangka	2	0	0
Billiton	3	0	0
Western Borneo	0	0	3
Eastern Borneo	1	0	0
Northern Borneo	2	0	0
"Borneo"	4	1	3
Central Java	4	2	95
Eastern Java	0	1	21
Bali	0	0	1

Table 43.—Frequency Distribution of Contact Between Prefrontal Scale and Eye Within Various Samples of *Calamaria schlegeli* Having Indicated Preocular Counts.

	Prefrontal-eye relationship		
	Touching	T/S	Separate
	Preocular count *1/1*		
Northern Malaya	2	0	9
Central Malaya	0	0	3
Singapore	0	0	10
Northern Sumatra (Deli)	0	0	2
Northern Sumatra (Tawar)	1	0	2
Western Sumatra	3	1	1
Southeastern Sumatra	1	0	3
Bangka	0	0	2
Billiton	1	0	2
Borneo	0	2	5
Java	4	0	1
	Preocular count *0/1*		
Western Sumatra	1	1	0
Southeastern Sumatra	1	0	0
Java	3	0	0
Borneo	0	1	0

smaller. The contact of prefrontal and eye is, therefore, a measure of preocular size. As shown in Table 43, all but one of the Javan snakes having preoculars have small ones (i.e., prefrontal touching eye). The preoculars in Sumatran snakes are roughly divided between large and small ones, those in Bornean and Malayan snakes are usually large, and those in Singapore specimens always large. Thus populations characterized by the absence of preoculars have small preoculars when present, those characterized by the presence of preoculars usually have large ones.

Within Sumatra local differentiation in the preoculars is suggested by the data in Tables 42 and 43. The relative frequencies of 0/0 preocular counts and of small preoculars in those individuals having them is greater in the extreme northern (Tawar Lake) and western (Bukit Tingi) Sumatran samples than in the others.

Head coloration (Fig. 41) also shows variation on a broad geographic scope as well as on a minor, local base (Table 44). Red-headed (pale yellow in preservative) snakes are the only type known from Singapore. All Javan specimens have black or brown heads without red or yellow extending dorsally (Fig. 43). The other samples are more variable, the greatest range being shown by the one from southeastern Sumatra. The northern Malayan sample consists of 8 snakes from Penang Island and 3 from Perak. The last are the 3 in column "D" while the Penang snakes are the ones in columns

TABLE 44.—Frequency Distribution of Types of Head Coloration Within Samples of *Calamaria schlegeli.*

	Head coloration*					
	A	B	C	D	E	F
Northern Malaya	4	4	0	3	0	0
Central Malaya	1	1	0	1	0	0
Singapore	0	0	0	0	0	10
Northern Sumatra (Deli)	0	0	1	0	0	1
Northern Sumatra (Tawar)	0	4	1	0	0	0
Western Sumatra	0	3	4	7	1	0
Southeastern Sumatra	0	2	1	0	1	1
Bangka	0	0	0	0	1	1
Billiton	0	0	0	3	0	0
Western Borneo	1	2	0	0	0	0
Eastern Borneo	0	0	0	0	0	1
Northern Borneo	2	0	0	0	0	0
Java	243	0	0	0	0	0
Bali	1	0	0	0	0	0

* Categories illustrated in Fig. 41, except "A," which has no light pigment, and "F," which has no dark pigment.

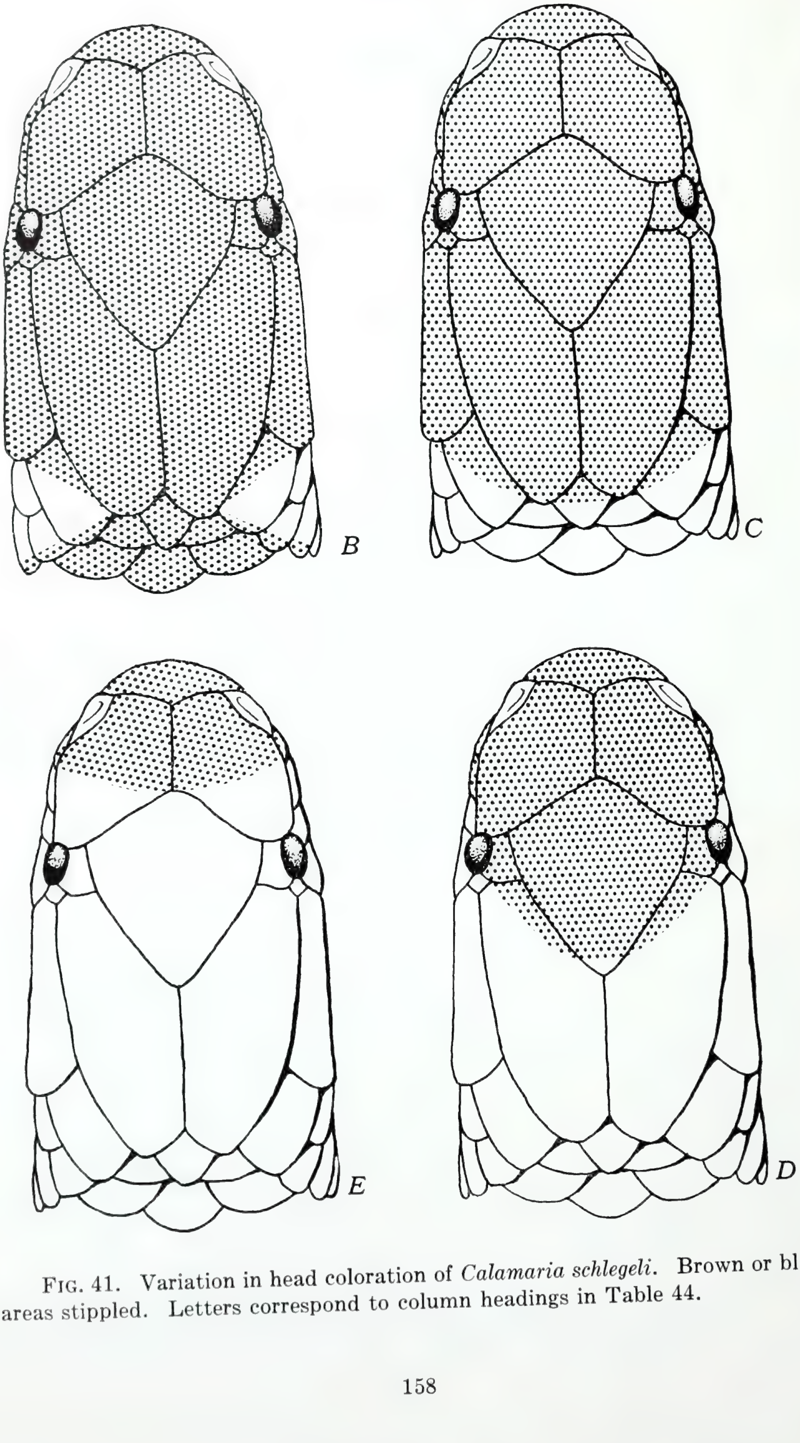

FIG. 41. Variation in head coloration of *Calamaria schlegeli*. Brown or black areas stippled. Letters correspond to column headings in Table 44.

"A" and "B" of Table 44, indicating local differentiation even within this relatively small part of the range.

Ventral and subcaudal counts vary locally though no overall macrogeographic pattern emerges (Table 45). Analyses of variation carried out using the samples having five or more specimens, show that the differences between those samples are statistically significant ($P<0.01$). The two large Javan samples differ from one another significantly ($P<0.05$) in these counts.

The ratio of tail length to total length shows the same pattern of variation as the number of subcaudals.

The point of reduction to four dorsal scale rows is closer to the tip of the tail in the Javan samples than in all of the others (Table 46). This character, which unlike subcaudal counts shows no sexual dimorphism, is not correlated with the number of subcaudals. The subcaudal counts of the Javan samples do not differ greatly from those of Malaya, for example, although the points of reduction do.

The posterior chin shields usually meet along the midline in this species, although in some specimens they are separated by a small gular scale. The frequency of separated chin shields is highest in the Sumatran sample (27 of 35 specimens), somewhat lower in the Bornean (6 of 14), and almost nonexistant in the other samples (4 of 152). There are three gulars in the midline anterior to the first ventral when the chin shields meet and four when they are separated. Only in a single Javan snake having separated chin shields do we find just three gulars.

Two specimens, a male (BM 82.11.27.2) and a female (BM 82.11.27.3), supposedly from Singapore differ radically in counts and head coloration from other Singapore snakes. They are the only two Singapore specimens having black instead of yellow heads. The male has 149 ventrals whereas the highest count in the other five males is 137; the questionable male has 29 subcaudals, 8 less than the nearest count among the other five. The female differs from five other Singapore females in the same way; its counts are 165 and 27, and the nearest in the other five are 153 and 31. Omitting these two black-headed specimens leaves narrow ranges of variation in ventral and subcaudal counts in the Singapore sample, a situation typical for the genus. In Table 45, for example, the Wonosobo, Java, sample of 44 males has a range of 11 ventrals, which is less than the difference between the counts of the questionable Singapore male and the closest male. The same comparison can be made for the female specimens.

Table 45.—Geographic Variation in Ventrals, Subcaudals, and Tail Ratio of *Calamaria schlegeli*.

	No.	Ventrals		Subcaudals		Tail ratio[1]	
		Range	Mean	Range	Mean	Range	Mean
				MALES			
Northern Malaya	5	140–51	146.0	29–32	30.4	127–146	137
Singapore	5	132–37	135.4	37–42	39.2	157–188	176
Northern Sumatra (Tawar)	2	142–43	142.5	34	..	150–153	152
Western Sumatra	4	130–40	134.8	27–29	28.0	120–136	126
Southeastern Sumatra	3	130–34	131.6	27–34	30.6	138–166	155
Billiton	2	134–36	135.0	34–37	35.5	147–153	150
Western Borneo	2	134–40	137.0	28	..	137–138	138
Eastern Borneo	1	136	..	34	..	156	..
Northern Borneo	2	134–35	134.5	44	..	213	..
Western Java	1	140	..	36	..	153	..
Central Java	44	145–55	149.6	28–33	31.0	111–148	134
Eastern Java	5	147–61	154.2	27–31	29.2	116–147	125
				FEMALES			
Northern Malaya	6	152–67	160.2	24–26	25.0	94–111	101
Central Malaya	3	149–63	155.3	25–28	26.3	101–112	108
Singapore	5	150–53	151.4	31–35	32.6	126–144	138
Northern Sumatra (Tawar)	3	155–59	157.3	24–27	25.3	99–107	103
Northern Sumatra (Deli)	2	151	..	29–32	30.5	118–129	124
Western Sumatra	4	142–52	148.5	21–25	22.5	91–113	98
Southeastern Sumatra	2	152	..	19–20	19.5	86	..
Bangka	2	157–61	159.0	23–26	24.5	97–105	101
Billiton	1	152	..	30	..	121	..
Western Borneo	1	169	..	28	..	99	..
Central Java	54	162–73	167.0	23–28	24.9	86–109	98
Eastern Java	10	169–80	175.8	23–27	23.8	73–106	81

[1] Ratio in thousandths of total length.

TABLE 46.—Geographic Variation in the Position of Reduction to Four Dorsal Scale Rows in *Calamaria schlegeli.*

	Number of subcaudals between level of reduction and terminal scute																						
	3	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*
	Number of males																						
Malaya												1		1	1				1				1
Singapore											1		1				2			1			
Sumatra									1	1	2	2	4		1		1		1				
Billiton															1				1				
Borneo											1			1			1		1				
Java	1		3	1	2	2	5	10	5	5	6	5	2	2									
	Number of females																						
Malaya													2	2		1		1					
Singapore												1	1	1				1	1				
Sumatra										2	3	2	3	1	1	1	2						
Bangka												1						1					
Billiton																							1
Borneo					1																		
Java	1		1	2	2	7	11	9	6	8	8	1		1									
Bali				1																			

On the basis of these differences in counts and coloration, we doubt the locality of the black-headed "Singapore" snakes, which were received by the British Museum from an unknown collector. The fact that for many years Singapore was the hub of traffic in the Indo-Malayan area and in particular was an important animal market lends some support to our suspicions. The counts and coloration of the doubtful specimens agree with those of Malayan snakes (Tables 44 and 45).

The data in Tables 43–46 show the Sumatran and Bornean samples to be more variable than the others. The greater range of variation in these two samples is evident in the preocular counts, head coloration, and in the relationship of the posterior chin shields. The Javan sample shows almost no variation in these three characters.

On the basis of differences in preoculars, in the position of the reduction to four dorsal scale rows, and in the consistently dark head coloration, we recognize the Javan and Bali samples as a distinct subspecies for which the name *cuvieri* Jan is available. Details of the differences are discussed above.

Calamaria schlegeli schlegeli Duméril and Bibron

Calamaria schlegeli Duméril and Bibron, 1854, Erp. Gén., **7**, p. 81—Borneo; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 8; 1865, Icon. Ophid., **10**, pl. 2, fig. 4; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 345; Bartlett, 1895, Sarawak Note Book, no. 1, p. 84; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 173; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173; de Haas, 1950, Treubia, **20**, p. 573; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 205.

Calamaria leucocephala Duméril and Bibron, 1854, Erp. Gén., **7**, p. 83—locality unknown; Günther, 1864, Rept. Brit. India, p. 198; Boulenger, 1894, *op. cit.*, p. 344 (part); Bartlett, *op. cit.*, p. 84 (part); Flower, 1896, Proc. Zool. Soc. London, **1896**, p. 886; **1899**, *ibid.*, p. 674; Brown, 1902, Proc. Acad. Nat. Sci. Philadelphia, **1902**, p. 694; Volz, 1904, Zool. Jahrb., (Syst), **20**, p. 497; Baumann, 1913, Zool. Jahrb., (Syst.), **34**, p. 271; de Rooij, *op. cit.*, p. 171 (part); Lidth de Jeude, 1922, Zool. Meded., **6**, p. 249; Mertens, 1924, Zool. Anz., **60**, p. 159; 1929, *ibid.*, **86**, p. 65; Lönnberg and Rendahl, 1925, Ark. Zool., **17A**, no. 23, p. 2; Werner, 1929, *loc. cit.*, p. 173 (part); Smith, 1930, Bull. Raffles Mus., no. 3, p. 58; Loveridge, 1938, Proc. Biol. Soc. Washington, **51**, p. 43; de Haas, *loc. cit.*, p. 569 (part); Tweedie, 1953, Snakes Malaya, p. 50, fig. 11d; Marx and Inger, *loc. cit.*, p. 203.

Calamaria agamensis Bleeker, 1860, Nat. Tijd. Ned. Indië, **21**, p. 292—Fort de Kock, Sumatra and Singkawang, Borneo; Günther, 1865, Ann. Mag. Nat. Hist., (3), **15**, p. 89; Boulenger, 1894, *op. cit.*, p. 343 (part); Bartlett, *op. cit.*, p. 84; de Rooij, *op. cit.*, p. 171 (part); Werner, 1929, *loc. cit.*, p. 173 (part); de Haas, *loc. cit.*, p. 563 (part).

Calamaria dumerili Bleeker, 1860, Nat. Tijd. Ned. Indië, **21**, p. 292—Singkawang, Borneo.

Calamaria sinkawangensis Bleeker, 1860, Nat. Tijd. Ned. Indië, **21**, p. 292—Singkawang, Borneo.

Calamaria roelandti Bleeker, 1860, Nat. Tijd. Ned. Indië, **21**, p. 294—Singkawang, Borneo.

Calamaria nigroalba Günther, 1864, Rept. Brit. India, pl. 18, fig. C—Penang Island.

Calamaria martapurensis Edeling, 1865, Ned. Tijd. Dierk., **2**, p. 203—Martapura, Borneo.

Calamaria iris Boettger, 1873, Ber. Offenb. Ver. Nat., **13**, p. 38, pl. 1—west coast of Sumatra.

Calamaria bicolor (non Duméril and Bibron), Mocquard, 1890, Nouv. Arch. Mus. Hist. Nat. Paris, (3), **2**, p. 135.

Keiometopon booliati Taylor, 1962, Univ. Kansas Sci. Bull., **41**, p. 258, figs. 16-17—Fraser's Hill, Malaya.

Holotype.—Rijksmuseum van Natuurlijke Historie 10424.

Diagnosis.—A preocular usually present; when preocular present, prefrontal usually separated from eye; head coloration varying from completely dark brown above to completely yellow (red in life); reduction to 4 dorsal scale rows opposite twelfth to twenty-fifth subcaudal anterior to terminal scute; posterior chin shields separated or meeting in midline.

Distribution.—Malaya to Sumatra and Borneo (Fig. 42).

MALAYA. Penang Island (BM 98.9.22.41, 1946.1.3.57-59—syntypes of *nigroalba*): Penang Hills (BM 97.2.3.6-7; NMS unnumbered), Government Hill (MHNP 91-203). Perak: Maxwell's Hill (NMS unnumbered), Taiping (ZMB 26458), Larut Hills (BM 1900.6.14.73). Pahang: Fraser's Hill (EHT-HMS M28—holotype of *K. booliati;* NMS 2 unnumbered). Selangor: Batu Caves (BM 98.9.22.40).

SINGAPORE (BM 82.11.29.2; CAS 16768; CNHM 72596; NMS 3 unnumbered): Bukit Timah (NMS 2 unnumbered), Naval Base (NMS 1 unnumbered), Nee Soon (MCZ 58878). ?Singapore (BM 82.11.27.2-3).

SUMATRA (AMNH 2878). Sumatera Utara: Bindjai (ZMH 2048), Deli (ZMA 10081), Sibolangit (NRS 2703), Lake Tawar (SNG 22431-35). Sumatera Tengah: Bukit Tinggi (BM 1946.1.3.60—holotype of *agamensis*, 1928.2.18.31-36), Singkarak (SNG 37823). Sumatera Selatan: Kaba Wetan (USNM 70953-54), Padang Highlands (RMNH 1863[3]), Padang Highlands, Muara Labu (RMNH 4688), Padang (NHMW 16712[7], 16999[2]), Palembang (NMB 5153), Bungar Bondar (SNG 19411-12).

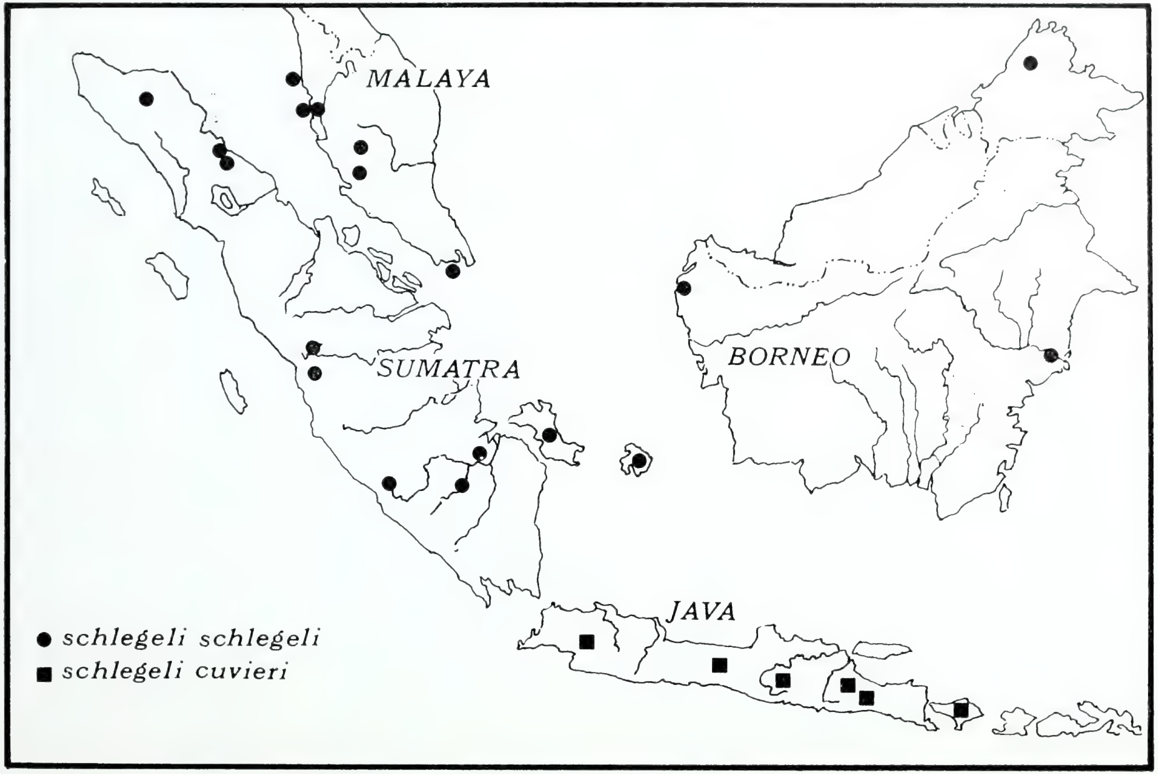

FIG. 42. Distribution of *Calamaria schlegeli*.

Bangka (RMNH 3753[2]).

Billiton (MHNP 4417; ZMA 10076[2]).

North Borneo: Mount Kina Balu (MCZ 43583; MHNP 89-190).

Indonesian Borneo: Singkawang (BM 63.12.4.30—holotype of *sinkawangensis,* 63.12.4.31—holotype of *roelandti,* 63.12.4.124— holo-of *dumerili*), Samarinda (ZMA 10079).

Borneo (BM 64.9.2.58; RMNH 10424—holotype; ZMB 4542[2], 8419, 9034; ZMH 4755; ZSBS 1933/0); central Borneo (SMNS 4586).

No locality data (CNHM 69976-79; RMNH 8733 [2]).

Specimens examined.—85.

Calamaria schlegeli cuvieri Jan. Figure 43.

Calamaria cuvieri Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 9—Java; 1865, Icon. Ophid. **10**, pl. 3, fig. 2.

Calamaria leucocephala (non Duméril and Bibron), Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 344 (part); Annandale, 1917, Jour. Fed. Malay States Mus., **7**, p. 107; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173 (part); Brongersma, 1930, Treubia, **12**, p. 302; Mertens, 1930, Abh. Senck. Naturf. Ges., **42**, p. 309; 1957, Senck. biol., **38**, p. 30; de Haas, 1950, Treubia, **20**, p. 569 (part).

Calamaria agamensis (non Bleeker), Boulenger, 1894, *op. cit.*, **2**, p. 343 (part); Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pl. 2, p. 84; Mertens, 1927, Senckenbergiana, **9**, p. 242; Werner, *loc. cit.*, p. 173 (part); Kopstein, 1941, Temminckia, **6**, p. 132; de Haas, *loc. cit.*, p. 563 (part).

Syntypes.—Museo Civico di Storia Naturale di Milano (not examined).

Diagnosis.—Preocular present in less than 6 per cent of specimens; prefrontal always touching eye; head always dark brown above; reduction to 4 dorsal scale rows opposite third to sixteenth subcaudal anterior to terminal scute; posterior chin shields meeting in midline.

Taxonomic notes.—Though Kopstein (1941) was correct in recognizing the differences between the Javan population and "*leucocephala,*" he erred in applying the name *agamensis* to the Javan form. The type localities of *agamensis* are in Sumatra and Borneo.

Distribution.—Java and Bali (Fig. 42).

Java (MCZ 8008; RMNH 10425; SNG 19409; ZMA 10080; ZMB 6937[4], 6938, 8759[2]); west Java (ZMA 10231[3]). Djawa Tengah: Sarangan (SNG 37821-22), Wonosobo, 800-1100 meters (RMNH

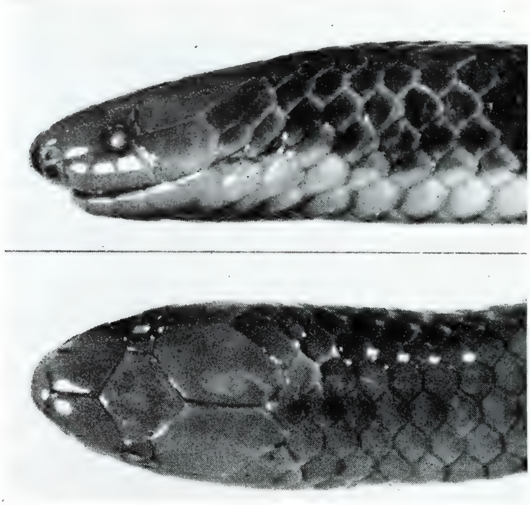

FIG. 43. *Calamaria schlegeli cuvieri* (CNHM 121033).

152 unnumbered), Wonosobo, Tlogodjati, ±1000 meters (RMNH 20 unnumbered), Wonosobo, Modjotengah, 1100 meters (RMNH 20 unnumbered), Wonosobo, Modjotengah, Lengkok, 1100 meters (RMNH 16 unnumbered), Pegelaran Estate (GM 3236[3]). Djawa Timur: Tengger Mountains (NHMW 16696[2]), Tengger Mountains, Nongkodjadiar, 1200 meters (CNHM 109948; RMNH 14 unnumbered), Malang (RMNH 5 unnumbered).

BALI: Baturiti (SNG 23333).

Specimens examined.—250.

Calamaria margaritophora Bleeker. Figure 44.

Calamaria margaritophora Bleeker, 1860, Nat. Tijds. Ned. Indië, **21**, p. 294—Ampat Lawang, Sumatra; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 156; Lidth de Jeude, 1922, Zool. Meded., **6**, p. 249; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 170; de Haas, 1950, Treubia, **20**, p. 570.

Calamaria maculolineata Peters, 1863, Monatsber. Akad. Wiss. Berlin, **1863**, p. 403—Kepahiang, Sumatra.

Calamaria margaritifera, Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 336, pl. 17, fig. 2; 1920, Jour. Fed. Malay States Mus., **8**, p. 290.

Calamaria hoevenii Edeling, 1870, Nat. Tijds. Ned. Indië, **31**, p. 380—Redjang, Sumatra; Boulenger, 1894, *op. cit.*, p. 337; de Rooij, *op. cit.*, p. 179; de Haas, *loc. cit.*, p. 568.

Calamaria margaritophora margaritophora, Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 203.

Syntypes.—British Museum (Natural History) 63.12.11.146 and Rijksmuseum van Natuurlijke Historie 3975a.

The original description lists "Java, Sumatra (Ampat Lawang)" as localities for *margaritophora.* The catalogues of the British Museum and Rijksmuseum do not give specific localities for the syntypes. As Bleeker does mention a specific locality, we believe the two syntypes were probably from that place and hereby restrict the type locality to Ampat Lawang, Sumatra.

Taxonomic notes.—Though we have not seen the holotype of *hoevenii,* we have examined two specimens (NHMW 16707; RMNH unnumbered) that fit the original description (Edeling, 1870) in all details. The only difference between these two "*hoeveni*" and *margaritophora* is in the presence of dark-edged, light dorsal crossbands. A Sumatran specimen (USNM 70952) has the pattern characteristic of *margaritophora* except that it has two interrupted yellow crossbands a short distance behind the head; at intervals of eight to ten scales this snake has five yellow vertebral spots that are increasingly narrow posteriorly. The pattern of this snake is an almost perfect intermediate between the banded "*hoeveni*" and the typical *margaritophora.* Boulenger (1894, p. 377) called attention to the strong similarity of *hoeveni* to *margaritophora* and suggested that the former was merely a color variety. The two snakes having the *hoeveni* pattern convince us that Boulenger was right.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 6 shields and scales; subcaudals of males 17 or fewer, of females 11 or fewer; without a continuous, dark vertebral stripe; tail thick, tapering abruptly near tip; ventrals of males 159 or fewer, of females 165 or fewer.

Description.—Rostral higher than wide, portion visible from above about equal to length of prefrontal suture; prefrontal about $^4/_5$ length of frontal, touching first 2 supralabials; frontal hexagonal, $1\frac{1}{2}$ to 2 times width of supraocular, slightly shorter than parietal; parietal about $1\frac{1}{3}$ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye equal to or greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal or fourth shortest; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting or not meeting in midline; three or four gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.020–0.045 (7 specimens); tail thick, tapering abruptly at end to blunt tip; dorsal scales reduce to 4 rows on tail opposite third to thirteenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fifth or sixth subcaudal, muscle begins opposite ninth subcaudal; sulcus spermaticus bifurcate; calyces papillate (2 specimens). Cloaca of female bilobed (1 specimen).

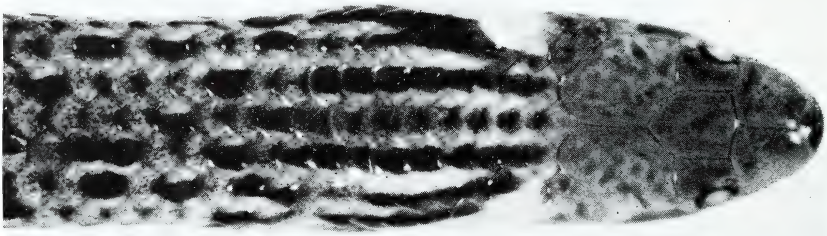

FIG. 44. *Calamaria margaritophora* (ZMB 8462).

Eight to 9 modified maxillary teeth (4 specimens).

Ventrals: males, 150–159 (mean 154.5; N=4); females, 147–163 (mean 156.8; N=6). Subcaudals: males, 13–17 (mean 15.5; N=4); females, 8–11 (mean 10.0; N=6).

Total length: males, 200–261 mm.; females, 256–358 mm. Ratio of tail to total length: males, 0.060–0.073 (mean 0.068; N=4); females, 0.034–0.047 (mean 0.041; N=6).

Color brown above, each scale above first row with a fine light network; a series of interrupted black lines formed by black spots in centers of many scales; black lines longest on neck; some individuals with narrow, light, dark edged crossbands; scale of first row with yellow centers forming a continuous light stripe; lower edge of first scale row and lateral margins of ventrals blackish brown forming a continuous dark stripe; tail dark brown above with one or two yellow triangles or spots low on sides; head dark brown above with obscure dark spots; supralabials yellowish except on upper margins; underside of head yellowish with a few small dark spots on sutures; ventrals yellow except for dark lateral margins; usually a few very small, widely scattered dark spots mid-ventrally; underside of tail yellow, usually immaculate, the lower color continuous with yellow spots on side of tail.

Distribution.—Southern Sumatra and possibly Java (Fig. 45).

SUMATRA (RMNH unnumbered; ZMB 8462). Sumatera Tengah: Siolak Daras, Korinchi, 945 meters (BM 1915.12.2.38), Kaba Wetan (USNM 70952). Sumatera Selatan: Ampat Lawang (BM 63.12.11. 146—syntype; RMNH 3975a—syntype), Rimbo Pengadang (RMNH 4689).

?Java (NHMW 16707; ZSI 14936). ?Batavia (MHNP 39-186).

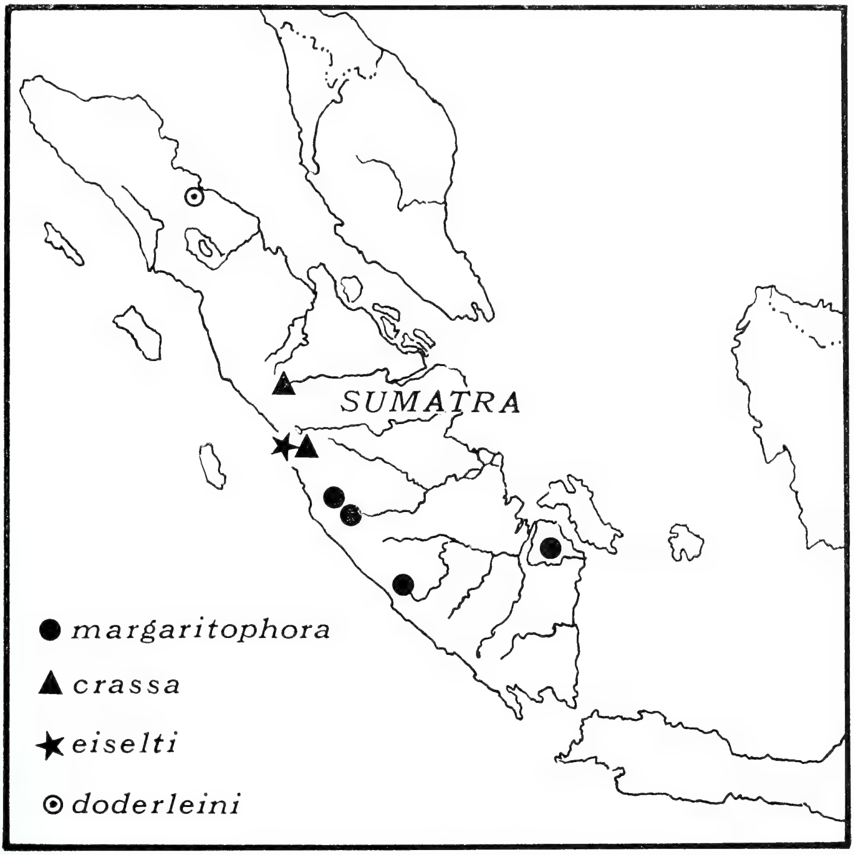

FIG. 45. Distributions of *Calamaria crassa*, *C. döderleini*, *C. eiselti*, and *C. margaritophora*.

The Paris Museum specimen (MHNP 39-186) from Batavia was collected by Baudart who also was the collector of a *C. lumbricoidea* (MHNP 39-187) with the locality Batavia. The latter specimen has all of the characteristics of the Sumatran and Bornean populations of *lumbricoidea* and differs radically from Javan *lumbricoidea.* As Batavia was for many years an important port in the East Indies, we suspect that Batavia was merely the port of embarkation for Baudart's specimens.

Specimens examined.—10.

Calamaria nuchalis Boulenger

Calamaria nuchalis Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **18**, p. 62—southern Celebes, 2000 feet; 1897, Proc. Zool. Soc. London, **1897**, p. 223, pl. 13, fig. 3; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 157; Werner, 1929, Zool. Jahrb., (Syst)., **57**, p. 170; de Haas, 1950, Treubia, **20**, p. 272; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 204.

Holotype.—British Museum (Natural History) 96.4.29.34.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; 6 scales and shields surrounding paraparietal; frontal as long as parietal; dark spots above third scale row not forming short longitudinal lines.

Description.—Head distinctly narrowed anteriorly; rostral higher than wide or as wide as high, portion visible from above ⅔ to greater than length of prefrontal suture; prefrontal ⅔ length of frontal, touching first 2 supralabials; frontal hexagonal, 1½ to 2⅔ times width of supraocular, equal to or longer than parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 6 (5 in 1 of 8 specimens) shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first smallest, other 3 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.008-0.034 (7 specimens); tail tapering gradually to a moderate point; dorsal scales reduce to 4 rows on tail opposite fourth to thirteenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth to fifth subcaudal, retractor beginning opposite seventh to ninth subcaudal, calyces smooth (3 specimens).

Nine to 10 modified maxillary teeth (3 specimens).

Ventrals: males, 133–146 (mean 141.1; N=7); female, 156. Subcaudals: males, 14–20 (mean 18.3; N=7); female, 9.

Total length: males, 123–294 mm.; female, 249 mm. Ratio of tail to total length: males, 0.077–0.100 (mean 0.087; N=7); female, 0.040.

Color brown above, each dorsal scale with a fine dark network; scattered dorsal scales with dark spot, spots not forming lines; scales of first row yellow in center forming continuous light stripe running length of body; a narrow dark stripe formed along adjacent edges of ventrals and first scale row; a dark stripe on second scale row; in a few specimens another dark stripe on third row; a light nuchal collar present or absent; head brown above with scattered dark spots, dark pigment ending along upper edge of supralabials; remainder of supralabials yellow, with or without dark sutures; underside of head yellow, immaculate or with dark sutures; ventrals yellow, immaculate except for dark lateral tips; underside of tail yellow, immaculate or with median brown stripe; tail above colored like body, some specimens with paired yellow spots laterally.

Distribution.—Central and southwestern Celebes (Fig. 29).

CELEBES (USNM 61193); southern Celebes, 610 meters (BM 96.4.29.34—holotype); Bua Praeng (NHMW 16715), Makale (RMNH 8382), Kulawi (GM 3225), Kantewu (GM 3224), Lake Lundu District (MCZ 45486), Pinedapa (USNM 61201).

Specimens examined.—8.

Calamaria boesemani new species

Holotype.—Naturhistoriska Museet Göteborg 3230, a female from Pinapuan (?Pinapolan) near Luwuk and Biak, near the tip of the eastern peninsula, Celebes. Collected by Walter Kaudern in December, 1919.

Diagnosis.—Maxillary teeth modified, third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; paraparietal surrounded by 6 shields and scales; nasals smaller than postocular and oriented laterally; eye very large, almost 1½ times eye-mouth distance.

Description.—Rostral wider than high, portion visible from above equal to length of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 2 times width of supraocular, about $^7/_8$ length of parietal; parietal almost twice length of prefrontal; paraparietal surrounded by 6 scales and shields; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye almost 1½ times eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first and third subequal and slightly shorter than the second and fourth which are subequal; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.009; tail thick, tapering at tip to a slightly elongated, compressed point; dorsal scales reduce to 4 rows on tail opposite the sixth subcaudal anterior to terminal scute.

Nine modified maxillary teeth.

Ventrals: 170; subcaudals: 16. Total length: 116 mm.; ratio of tail length to total length: 0.060.

Body brown above with many yellow and darker brown scales giving the appearance of very irregular wavy crossbands or squares; this coloration also present on the distal portion of the parietals; upper half of first scale row yellow forming a continuous light stripe the entire length of the body, the light stripe bordered above and below by continuous dark brown stripes on the lower half of the first scale row and the second scale row; head brown above with darker spots; upper one-third of supralabials dark brown, lower two-thirds yellow; head below yellow with very few dark brown spots; belly completely yellow; tail colored above and below like body except for a few dark brown spots at its ventral tip.

Comparisons.—*Calamaria boesemani* differs from the following Celebesian species in having the mental separated from the chin shields: *acutirostris, curta, apraeocularis, nuchalis,* and *muelleri.* The first two also differ from *boesemani* in having unmodified maxillary teeth; *apraeocularis* is further distinguished from *boesemani* by the absence of the preocular; and *nuchalis* has the frontal as long as the parietal. Conparison with *muelleri* appears on p. 100.

The two Celebesian species agreeing with *boesemani* in the relation of mental and chin shields are *brongersmai* and *virgulata.* Comparison with *brongersmai* appears on p. 119. The holotypes of *brongersmai* and *boesemani* were collected at the same place.

Calamaria virgulata differs from *boesemani* in having a smaller eye, greater number of ventrals, relatively shorter and thicker tail, and a smaller portion of the rostral visible from above.

The species agreeing with *boesemani* in having the mental separated from the chin shields, 5 supralabials, a preocular, modified maxillary teeth, and 6 scales and shields surrounding the paraparietals are *döderleini, lumholtzi, schlegeli, modesta,* and *virgulata.* All of these species differ from *boesemani* in having much smaller eyes and less of the rostral visible from above. Comparison with *virgulata* is in the preceding paragraph.

Calamaria döderleini also differs from *boesemani* in having an extremely short head and the nasals oriented forward; *lumholtzi* in having a light stripe on the second and third scale rows; *schlegeli* in having more subcaudals and a wider frontal; and *modesta* in having a longer parietal and no continuous lateral white stripe.

Distribution.—Extreme eastern Celebes (Fig. 29).

Calamaria crassa Lidth de Jeude. Figure 46.

Calamaria crassa Lidth de Jeude, 1922, Zool. Meded., **6**, p. 248—Mount Talakmau, Ophir District, Padang Highlands, 1300 m., Sumatra; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171; de Haas, 1950, Treubia, **20**, p. 566; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 201.

Holotype.—Rijksmuseum van Natuurlijke Historie 4692.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; 6 shields and scales surrounding paraparietal; ventrals in posterior half of body dark with narrow yellow margins; tail midventrally with dark stripe; ventrals of males fewer than 155, of females fewer than 165.

Description.—Rostral wider than high, portion visible from above equal to about half length of prefrontal suture; prefrontal $3/4$ to $4/5$ length of frontal, touching first 2 supralabials; frontal hexagonal, $1\frac{1}{2}$ to $2\frac{1}{3}$ times width of supraocular, about $5/6$ to equal length of parietal; parietal about $1\frac{1}{3}$ times length of prefrontal; paraparietal surrounded by 6 scales and shields; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.012–0.051 (8 specimens); tail thick, tapering abruptly near end to blunt tip; dorsal scales reduce to 4 rows on tail opposite second to tenth subcaudal anterior to terminal scute.

Hemipenis forked opposite sixth subcaudal; retractor muscle beginning opposite tenth subcaudal; calyces papillate distally (1 specimen). Cloaca of female bilobed (2 specimens).

Ten modified maxillary teeth (7 specimens).

Ventrals: males, 136–154 (mean 146.3; N=4); females, 158–164 (mean 161.8; N=5). Subcaudals: males, 21–28 (mean 25.5; N=4); females, 14–17 (mean 15.0; N=5).

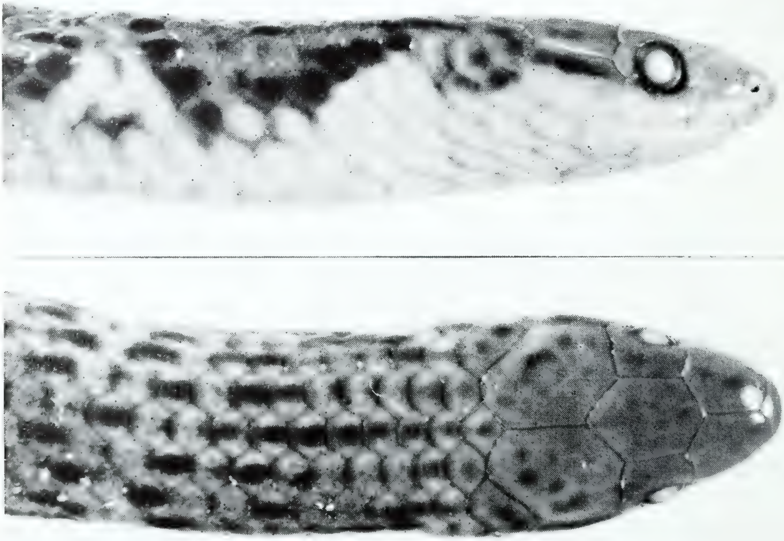

FIG. 46. *Calamaria crassa* (RMNH 34).

Total length: males, 131–436 mm.; females, 227–372 mm. Ratio of tail to total length: males, 0.095–0.129 (mean 0.113; N=4); females, 0.057–0.061 (mean 0.059; N=5).

Color brown above with scattered dark spots forming short longitudinal streaks; most dorsal scales with a fine dark network; behind twentieth ventral scales of first row with light centers; head brown above with obscure dark spots; dark pigment extending on to upper half or upper edges of supralabials, larger specimens with dark spots on first 2 supralabials; underside of head yellow with a few dark spots on scale sutures; first 10 to 20 ventrals yellow, yellow extending upward onto first 3 scale rows at 2 or 3 points forming light lateral triangles; behind tenth ventral brown spots appear on anterior edges of ventrals near their centers; brown area on ventrals becomes more extensive posteriorly on body and occupies all except a narrow posterior margin or a yellow semicircular area near lateral corners; underside of tail yellowish with a broad midventral dark streak or with scattered dark spots along the midline; outer edges of subcaudals usually dark.

A juvenile (168 mm., RMNH unnumbered) has a series of narrow yellowish rings (1 scale wide) crossing dorsum at intervals of 6 to 10 scales.

Distribution.—West central Sumatra (Fig. 45).

SUMATRA (CNHM 134230; RMNH 34[4], 1 unnumbered; ZMB 5229). Sumatera Tengah: Padang (NHMW 16994), Ophir District, Mount Talakmau, 1300 meters (RMNH 4692—holotype).

Specimens examined.—9.

Calamaria eiselti new species. Figure 47.

Holotype.—Naturhistorisches Museum Wien 16703:1, an adult male from Padang, Sumatra, collector unknown.

Paratypes.—Naturhistorisches Museum Wien 16703:2–4, 16701:1, Chicago Natural History Museum 134723, all from Padang, Sumatra.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental in contact with anterior chin shields; paraparietal surrounded by 6 shields and scales; ventrals in posterior half of body blackish with small yellow spots; underside of tail yellow with 1 to 3 complete or incomplete black crossbands.

Description.—Rostral wider than high, portion visible from above $\frac{1}{2}$ to $\frac{2}{3}$ length of prefrontal suture; prefrontal $\frac{3}{4}$ to equal length of frontal, touching first 2 supralabials; frontal hexagonal, $1\frac{1}{2}$ to $1\frac{4}{5}$ times width of supraocular, about $\frac{3}{4}$ to $\frac{4}{5}$ length of parietal; parietal $1\frac{1}{2}$ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye slightly greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.029–0.099 (6 specimens); tail thick, tapering near end to a blunt tip.

Hemipenis forked opposite sixth or seventh subcaudal: sulcus spermaticus forked; calyces smooth (2 specimens). Cloaca of female weakly bulbous (1 specimen).

Ten modified maxillary teeth (3 specimens).

See Table 47 for counts.

Color dark brown above, each dorsal scale finely speckled with yellow; a few scattered scales solid dark brown; no scales with dark centers; some scales of first row with light centers; top of head same color as body, without spots; dark pigment extending down to cover

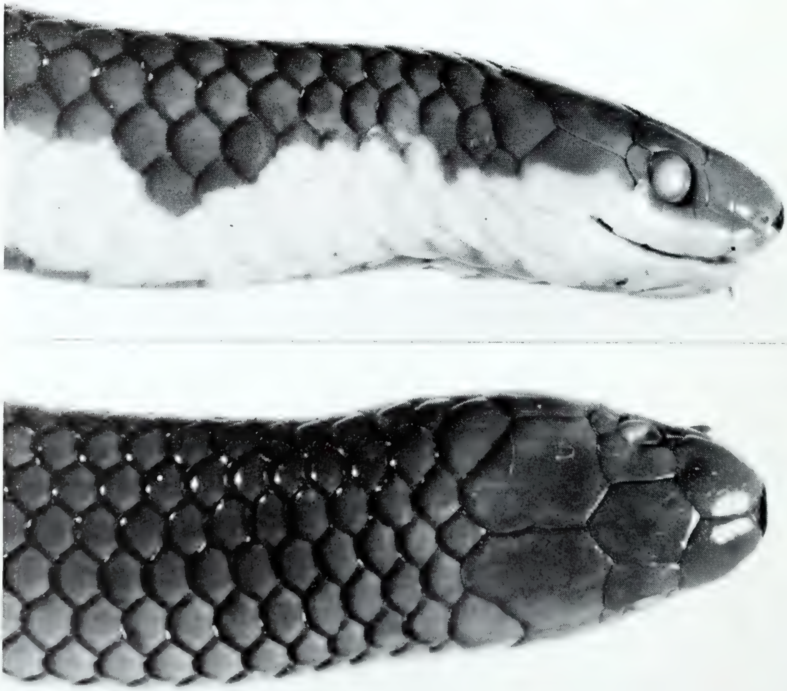

FIG. 47. Paratype of *Calamaria eiselti* (NHMW 16703:4).

TABLE 47.—Individual Variation of Certain Characters of *Calamaria eiselti*.

Museum no.	Sex	Ventrals	Sub- caudals	Reduction*	Total length, mm.	Tail ratio
NHMW 16703:1	♂	137	21	13	343	0.102
NHMW 16703:4	♂	137	22	13	333	0.105
NHMW 16703:2	♀	151	15	6	424	0.068
NHMW 16703:3	♀	151	13	5	365	0.063
CNHM 134723	♀	151	14	7	381	0.063
NHMW 16701:1	♀	153	14	7	244	0.061

* Reduction to four dorsal scale rows; position in terms of subcaudals counted from vent.

upper half or third of supralabials; underside of head yellowish with dark spots on scale sutures; a broad yellow band continuous with yellow of lips covering lateral third or fourth of ventrals and first and second scale rows and extending back to the level of the tenth to twentieth ventral; yellow band may be interrupted by ventral extensions from dark dorsal pigmentation; anteriorly ventrals usually with a black central area separating lateral yellow bands; behind tenth to twentieth ventral belly black with scattered, small, semicircular yellow spots, usually 2 spots per ventral; dark ventral pigmentation usually ends abruptly with anal plate; underside of tail yellow with one to 3 complete or interrupted black crossbands; only one of 6 specimens lacks these crossbands.

Comparisons.—The following species of *Calamaria* have 5 supralabials, a preocular, mental touching anterior chin shields, 6 scales and shields surrounding the paraparietals, and modified maxillary teeth in common with *eiselti*: *sumatrana, crassa, margaritophora, virgulata, nuchalis, forcarti,* and *abstrusa.*

Calamaria eiselti differs from all of these species in ventral coloration; it is the only form having a black belly and the only one having a yellow tail marked with black crossbars. It also has a conspicuously thicker body than any other species (see Table 13, Fig. 11).

Calamaria eiselti is sympatric in the Padang areas with the following species: *sumatrana, crassa, alidae, lumbricoidea, modesta, schlegeli,* and *abstrusa.*

Distribution.—West-central Sumatra (Fig. 45).

Calamaria döderleini Gough. Figure 48.

Calamaria döderleini Gough, 1902, Zool. Anz., **25**, p. 645—Langkat, Sumatra; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 172; Werner, 1929, Zool.

Jahrb., (Syst.), **57**, p. 173; de Haas, 1950, Treubia, **20**, p. 566; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 201.

Holotype.—Musée Zoologique de l'Université, Strasbourg, unnumbered.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental not touching anterior chin shields; paraparietals surrounded by 6 shields and scales; belly with dark crossbands, each more than 1 ventral wide.

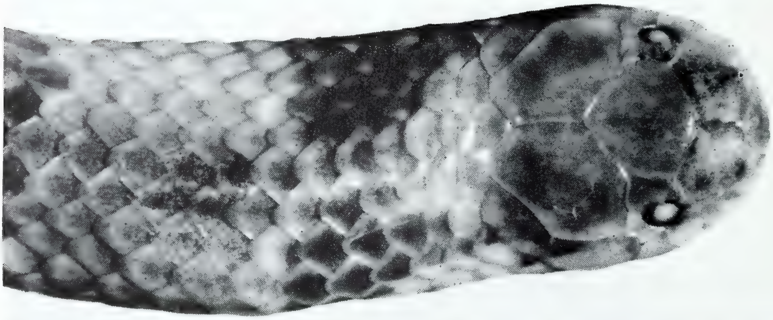

FIG. 48. Holotype of *Calamaria döderleini.*

Description.—Head very short and rounded; rostral slightly higher than broad, portion visible from above almost equal to length of prefrontal suture; prefrontal slightly shorter than frontal, touching first 2 supralabials; frontal hexagonal, 2 $^4/_5$ times width of supraocular, about $^4/_5$ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular, oriented forward; preocular present, not as high as eye; postocular as high as eye; eye ⅔ eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, fourth narrowest, and first, second, and third subequal; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.038; tail thick, tapering abruptly to a round tip; dorsal scales reduce to 4 rows on tail opposite sixth subcaudal anterior to terminal scute.

Ten modified maxillary teeth.

Ventrals 163 in male; subcaudals 20. Total length of male 288 mm.; ratio of tail length to total length 0.083.

Body and tail light brown with 25 narrow dark brown crossbands (23 on body, 2 on tail) one dorsal scale wide and separated from each other by 5 to 9 scales; scales of interspaces with dark network; head light brown above, dark pigment extending to upper fifth of supralabials; supralabials and underside of head yellow; belly yellow with bold dark brown crossbands, each usually occupying 1½ or 2 ventrals; ventral bands separated by 2 to 5 ventrals, closer together in posterior half of body; tail above and below like body.

Distribution.—Northeastern Sumatra (Fig. 45).

SUMATRA. Sumatera Utara: Langkat (MZUS unnumbered—holotype).

Calamaria abstrusa[1] new species. Figure 49.

Calamaria sumatrana (non Edeling), Boulenger, 1894, Cat. Snakes Brit. Mus., **3**, p. 340 (part); Werner, 1896, Verh. Zool. Bot. Ges. Wien., **46**, p. 18.

Holotype.—Naturhistorisches Museum Wien 17026, an adult male from Padang, Sumatra collected by J. Schild.

Paratype.—USNM 35795 from Nias; ZMB 12028 from Sumatra; BM 64.4.7.11[2] probably from Sumatra; ZMB 5986[2] from "East Indies."

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 6 shields and scales; ventrals yellow or white except at lateral edges; subcaudals of males more than 20, of females more than 13; no continuous vertebral stripe; ventrals less than 160 in both sexes.

Description (counts and measurements of holotype in parentheses).—Rostral wider than high, portion visible from above ½ length of prefrontal suture; prefrontal ⅔ length of frontal, touching first 2 supralabials; frontal hexagonal, 1¾ to $2^4/_5$ times width of supraocular, about ⅞ length of parietal; parietal almost twice length of prefrontal; paraparietal surrounded by 6 shields and scales, by 5 on one side of one specimen; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye about 1½ times eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

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[1] *Abstrusa,* (L.) hidden, concealed. Referring to the concealment of the true identity of this species under the name *C. sumatrana.*

Body thickness index 0.011–0.012 (3 specimens); tail thick, tapering near end to a point; dorsal scales reduce to 4 rows on tail opposite third to seventh subcaudal anterior to terminal scute.

Hemipenis forked opposite seventh subcaudal; retractor muscle beginning opposite eleventh subcaudal; calyces smooth (1 specimen).

Eight to 9 modified maxillary teeth (4 specimens).

Ventrals: males, 129–148 (mean 135.6; N=5) (130); females, 145–152 (N=2). Subcaudals: males, 24–25 (mean 24.2; N=5) (25); females, 14 (N=2).

Total length: males, 159–170 mm. (170); females, 191–209 mm. Ratio of tail to total length: males, 0.099–0.124 (mean 0.115: N=5) (0.124); females, 0.062–0.063 (N=2).

Color brown above, each dorsal scale lighter in center than at edges; scattered scales with a dark central spot, those in second row forming a more or less continuous stripe; dark spots on vertebral scale row not forming a continuous stripe; a yellow ring 1 to 2 scales wide separated from parietals by 5 or 6 scales; each scale between parietals and yellow ring with a dark central spot; head dark brown above with obscure darker spots; lower half of supralabials yellow, underside of head yellow with a few faint brown spots; ventrals yellow, immaculate except for dark lateral margins; tail above colored like body, without yellow spots; underside of tail yellow, with or without a yellowish brown streak.

Comparisons.—This species and *eiselti*, *crassa*, *margaritophora*, *nuchalis*, *forcarti*, and *sumatrana* have the following characters in common: modified maxillary teeth, third and fourth supralabials touching the eye, preocular present, mental touching chin shields, and 6 scales surrounding the paraparietal. *Calamaria eiselti*, *crassa*, and *margaritophora* have much thicker bodies than *abstrusa* and the first 2 also differ from *abstrusa* in having dark pigment across the middle of the ventrals. *Calamaria margaritophora* has fewer subcaudals (males fewer than 17, females fewer than 11) than *abstrusa*. *Calamaria nuchalis* has fewer subcaudals (males fewer than 20, female 9) and a relatively longer frontal than *abstrusa*. *Calamaria forcarti* has more ventrals and subcaudals than *abstrusa*.

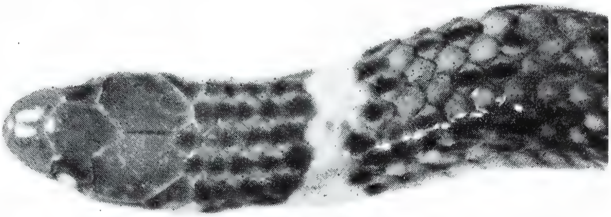

FIG. 49. Holotype of *Calamaria abstrusa.*

Calamaria sumatrana is similar to *abstrusa* and is sympatric with it at least in the Padang area of Sumatra. These two species differ in coloration, relative tail length, and in the position of the reduction to four dorsal scale rows. *Calamaria sumatrana* has yellow spots on the sides opposite the vent and a narrow continuous vertebral stripe; neither of these markings is present in *abstrusa.* The ratio of tail length to total length in *sumatrana* is 0.063–0.088 in males, and 0.040–0.047 in females; in *abtrusa* it is 0.099-0.124 in males, and 0.062–0.063 in females. The subcaudals of *sumatrana* are 14–20 in males, 10–14 (1 of 11 has 14) in females; in *abstrusa* they are 24–25 in males, and 14 in females.

Distribution.—Nias and western Sumatra (Fig. 50).

Calamaria sumatrana Edeling. Figure 51.

Calamaria sumatrana Edeling, 1870, Nat. Tijds. Ned. Indië, **31**, p. 379—Redjang, Sumatra; Boulenger, 1890, Proc. Zool. Soc. London, **1890**, p. 34; 1894, Cat. Snakes Brit. Mus., **2**, p. 339; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 83; Cohn, 1905, Zool. Anz., **29**, p. 545; Lange and de Rooij, 1910, *in* Maass, Durch Zentral Sumatra, **2**, p. 516; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 157 (part); Robinson and Kloss, 1920, Jour. Fed. Malay States Mus., **8**, p. 301; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 170 (part); de Haas, 1950, Treubia, **20**, p. 574 (part); Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 206.

Calamaria pavimentata (non Duméril and Bibron), Müller, 1885, Verh. Naturf. Ges. Basel, **7**, p. 678; Boettger, 1887, Ber. Senck. Naturf. Ges., **1887**, p. 53.

Neotype.—Zoologisch Museum Amsterdam 10237, from Deli, Medan, Sumatra.

Edeling's two syntypes have apparently been lost. We have inquired about his material at the Museum Zoologicum Bogoriense,

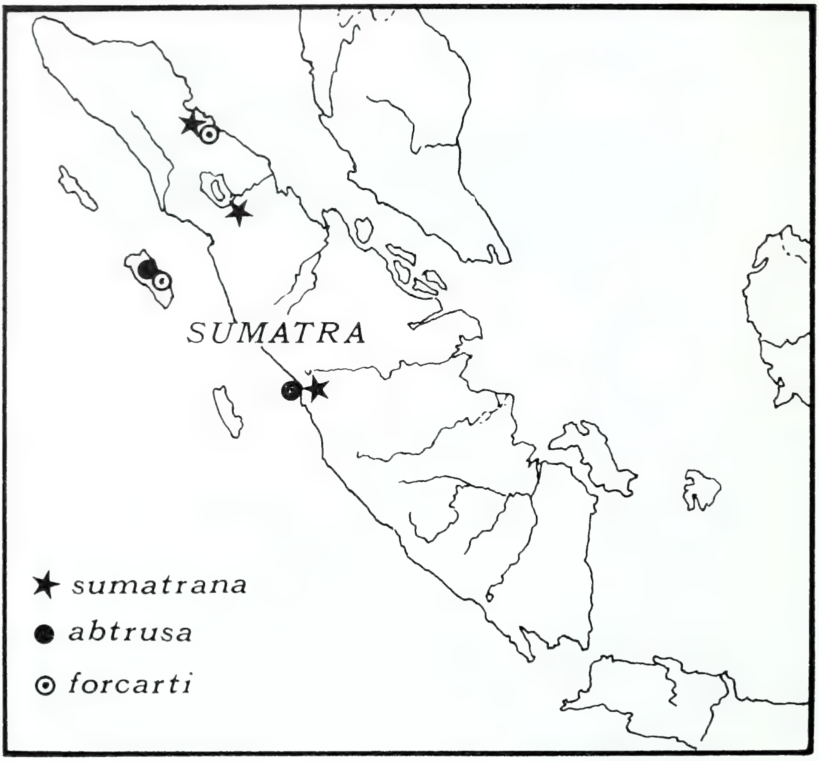

FIG. 50. Distributions of *Calamaria abstrusa*, *C. forcarti*, and *C. sumatrana*.

Java, and director at the time, Mr. A. M. R. Wegner, informed us that Edeling's collection is not in Bogor. None of the major European institutions has his material.

Since *sumatrana* is not one of the well known species of *Calamaria*, we believe it is wise to designate a neotype. The specimen selected agrees with the original description.

The female neotype has 164 ventrals, 10 subcaudals, a total length of 227 mm., and a tail length of 9 mm.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietals surrounded by 6 shields and scales; ventrals yellow or white except at lateral edges; a continuous dark vertebral stripe.

Four of 17 *sumatrana* have interrupted vertebral stripes. The only species with which these 4 specimens can be confused is *mar-*

garitophora which is about twice the thickness of *sumatrana.* Three of these 4 fall outside the range of variation of ventral and subcaudal counts of *margaritophora.*

Description.—Rostral broader than high or higher than broad, portion visible from above equal to ½ to ⅔ length of prefrontal suture; prefrontal ¾ to ⁵/₆ length of frontal, touching first 2 supralabials; frontal hexagonal, 1⅔ to 2½ times width of supraocular, about ¾ length of parietal; parietal 1½ to 1⅔ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye equal to or slightly greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

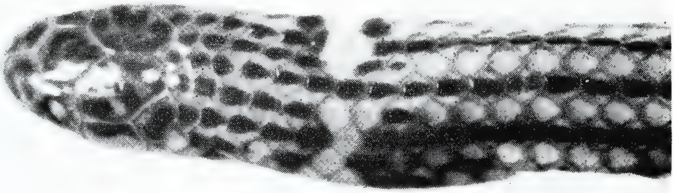

FIG. 51. *Calamaria sumatrana* (ZMH 3996).

Body thickness index 0.010–0.018 (9 specimens); tail thick, tapering abruptly near end to a blunt tip; dorsal scales reduce to 4 rows on tail opposite second to eighth subcaudal anterior to terminal scute; 1 specimen (ZMH 3996) has 6 scale rows at terminal scute.

Hemipenis forked opposite fifth to seventh subcaudal; retractor muscle beginning opposite seventh to ninth subcaudal; calyces smooth (3 specimens).

Eight to 9 modified maxillary teeth (6 specimens).

Ventrals: males, 126–157 (mean 145.8; N=6); females, 164–175 (mean 169.5; N=11). Subcaudals: males, 14–20 (mean 17.7; N=6); females, 10–14 (mean 12.0; N=11).

Total length: males, 101–222 mm.; females, 184–258 mm. Ratio of tail to total length: males, 0.069–0.088 (mean 0.081; N=6); females 0.040–0.047 (mean 0.043; N=10).

Color dark brown above; each scale above second row with fine dark network or with a black central spot; black spot present on every scale immediately behind head as far as yellow neck ring; behind neck ring 3 to 5 more or less distinct black lines formed by black spots on second, fifth and the vertebral scale rows; scales of first row with whitish centers forming a longitudinal stripe to vent; yellow neck ring formed by extension of light ventral color dorsally 5 to 7 scales behind parietals; a large yellow spot or a narrowly interrupted yellow ring on side of body opposite vent; a similar pair of spots near tip of tail usually present; top of head brown with obscure black spotting; dark pigment reaches upper third of supralabials and extends to lip along labial sutures; underside of head yellowish with dark spots on anterior infralabials and chin shields; ventrals immaculately cream color or yellow, with dark outer edges; underside of tail yellowish with a dark midventral stripe.

Distribution.—Sumatra (Fig. 50).

SUMATRA (AMNH 2873; ZSBS 2660/0). Sumatera Utara; Bindjai (ZMH 2466), Deli district (BM 89.11.12.15), Deli (NMB 1702; RMNH 4860; SNG 19400; ZMA 10238–39), Deli, Medan (CNHM 83465; ZMA 10237—neotype), Sibulangit (NHMW 16995), Balige (MCG 30382). Sumatera Tengah: Padang area, Bobangan (ZMH 3996[2]); Tandjong (ZMH 2307); east Sumatra, Sukaranda (NHMW 16711).

Specimens examined.—17.

Calamaria forcarti new species

Calamaria stahlknechtii (non Stoliczka), Roux, 1925, Rev. Suisse de Zool., **32**, p. 319.

Holotype.—Naturhistorisches Museum Wien 16710, a male from Deli, Sumatra, collector unknown.

Paratypes.—NHMW 16709, a female from the type locality, NMB 8958, a male from Nias, and ZMA 10073, a female from Lelewoea, Nias.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; preocular present; mental touching anterior chin shields; paraparietal surrounded by 6 shields and scales; ventrals more than 175 in males, 190 in females; body slender without stripes; venter yellow; narrow dark crossbands behind head.

Description (data on holotype in parentheses).—Rostral wider than high, portion visible from above about half length of prefrontal suture; prefrontal about ¾ length of frontal, touching first 2 supralabials; frontal hexagonal, 1¾ to 1⅞ times width of supraocular, about ¾ length of parietal; parietal 1⅔ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye greater than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first 4 subequal; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.008–0.009 (3 specimens); tail tapering gradually to a blunt tip; dorsal scales reduce to 4 rows on tail opposite seventh to thirteenth (thirteenth) subcaudal anterior to terminal scute.

Hemipenis unforked with smooth calyces (2 specimens).

Eight modified maxillary teeth (2 specimens).

Ventrals: males, 176–177 (N=2) (177); females, 194–200 (N=2). Subcaudals: males, 30 (N=2); females, 16–17.

Total length: males, 216–239 (239) mm.; females, 235–288 mm. Ratio of tail to total length: males, 0.117–0.120 (0.117); females, 0.052–0.060.

Body and tail pale brownish above; most dorsal scales with a faint, dark network; scattered dark brown spots dorsally, each spot occupying 1 to 4 scales; spots arranged in transverse rows rather than longitudinal ones; a yellow ring 5 to 7 scales behind parietals, ring bordered anteriorly and posteriorly with blackish brown bands 1 to 2 scales wide; 1 to 3 complete or narrowly interrupted light, dark-edged rings across dorsal surface of tail; head brown above with obscure darker markings; supralabials dark brown on upper third, yellowish near lip with scattered dark spots; head below yellow with dark spots on infralabials and anterior chin shields; ventrals yellowish, immaculate, or with widely scattered minute brown spots; usually extreme lateral edges of ventrals brown; underside of tail immaculate yellow except for dark brown lateral edges of subcaudals.

Comparisons.—The following species of *Calamaria* have 5 supralabials, a preocular, mental touching anterior chin shields, 6 scales surrounding the paraparietal, and modified maxillary teeth, in common with *forcarti*: *sumatrana, abstrusa, crassa, eiselti, margaritophora, nuchalis,* and some *virgulata* from Celebes. The dorsal spots, which tend to form transverse bands, distinguish *forcarti* from all of these except *margaritophora.*

Calamaria forcarti differs from *crassa, eiselti,* and *margaritophora* in having a much more slender body and more ventrals and subcaudals.

Calamaria forcarti has more subcaudals than *sumatrana, virgulata, abstrusa,* and *nuchalis. Calamaria forcarti* also differs from *nuchalis* and *virgulata* in having less of the rostral reflected onto the top of the snout. It also lacks the dorsal stripes characteristic of *sumatrana* and has many more ventrals than *sumatrana* and *abstrusa.*

At Deli, Sumatran *forcarti* is sympatric with *leucogaster, mecheli, schlegeli, lumbricoidea,* and *sumatrana. Calamaria leucogaster* has unmodified maxillary teeth; *mecheli* and *schlegeli* have the mental separated from the chin shields, much wider frontals, and much smaller eyes; *lumbricoidea* has only 5 scales surrounding the paraparietal and lacks dark dorsal spotting.

Distribution.—Northern Sumatra and Nias (Fig. 50).

Calamaria virgulata H. Boie. Figure 52.

Calamaria virgulata H. Boie, *in* F. Boie, 1827, Isis, **20**, p. 540—Java; Lidth de Jeude, 1890, Notes Leyden Mus., **12**, p. 254.

Calamaria modesta (non Duméril and Bibron), F. Müller, 1894, Verh. Naturf. Ges. Basel, **10**, p. 2.

Calamaria brachyura Boulenger, 1895, Ann. Mag. Nat. Hist., (6), **16**, p. 481—Mount Kina Balu, North Borneo; 1896, Cat. Snakes Brit. Mus., **3**, p. 647; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 167; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 172; de Haas, 1950, Treubia, **20**, p. 565; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 192.

Calamaria anceps Werner, 1896, Verh. Zool. Bot. Ges. Wien, **46**, p. 18—Sumatra.

Calamaria gracilis Boulenger, 1896, Ann. Mag. Nat. Hist., (6), **18**, p. 63—Mount Bonthain, Celebes; 1897, Proc. Zool. Soc. London, **1897**, p. 224, pl. 14, fig. 3; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 86; de Rooij, *op. cit.*, p. 159; Smith, 1927, Proc. Zool. Soc. London, **1927**, p. 223; Werner, 1929, *loc. cit.*, p. 171; de Haas, *loc. cit.*, p. 567; Marx and Inger, *loc. cit.*, p. 202.

Calamaria collaris Boulenger, 1897, Proc. Zool. Soc. London, **1897**, p. 225, pl. 14, fig. 4—Bone Mountains, Tomohon, Rurukan, Celebes; Boettger, *loc. cit.*, p. 84; de Rooij, *op. cit.*, p. 167; Werner, 1929, *loc. cit.*, p. 172; de Haas, *loc. cit.*, p. 565; Marx and Inger, *loc. cit.*, p. 201.

Calamaria mearnsi Stejneger, 1907, Smithsonian Misc. Coll., **50**, p. 30—Tangob, Mindanao, Philippine Islands; Taylor, 1922, Snakes Philip. Ids., p. 193; Werner, 1929, *loc. cit.*, p. 172; Marx and Inger, *loc. cit.*, p. 204; Leviton, 1963, Proc. Calif. Acad. Sci., **31**, p. 393.

Calamaria albopunctata Barbour, 1908, Bull. Mus. Comp. Zool., **51**, p. 319—East Indies; 1912, Mem. Mus. Comp. Zool., **44**, p. 121; de Rooij, *op. cit.*, p. 165; Werner, 1929, *loc. cit.*, p. 172; de Haas, *loc. cit.*, p. 563; Marx and Inger, *loc. cit.*, p. 199.

Calamaria quinquetaeniata Despax, 1912, Bull. Mus. Hist. Nat. Paris, **18**, p. 203—East Indies; de Rooij, *op. cit.*, p. 167; Werner, 1929, *loc. cit.*, p. 172; de Haas, *loc. cit.*, p. 573; Marx and Inger, *loc. cit.*, p. 205.

Calamaria egregia Barbour, 1927, Proc. Biol. Soc. Washington, **40**, p. 127—Mount Tibang, Borneo; de Haas, *loc. cit.*, p. 566; Marx and Inger, *loc. cit.*, p. 201.

Calamaria zamboangensis Leviton, 1952, Jour. Washington Acad. Sci., **42**, p. 239, fig. 1—Zamboanga, Mindanao, Philippine Islands; Marx and Inger, *loc. cit.*, p. 207; Leviton, 1963, *loc. cit.*, p. 393.

Holotype.—Rijksmuseum van Natuurlijke Historie 39.

Taxonomic notes.—The holotype of *anceps* from Sumatra is identical to the Bornean samples ("*brachyura*") in details of coloration, in counts, and in body proportions; no basis exists for separating these two populations. Similarly, the holotype of *albopunctata* ("East Indies") is identical to Celebes samples ("*collaris*"), and the holotype of *quinquetaeniata* ("East Indies") with *zamboangensis* (Mindanao).

Barbour (1927) gave incorrect ventral counts (202) for the holotype of *egregia;* the correct count is 194. This snake (MCZ 22648) is indistinguishable from Bornean "*brachyura.*"

All the specimens listed in Boulenger's catalogue (1894) and those identified by various authors since 1894 as *virgulata* are *modesta* (see p. 139); the holotypes of these two species were compared directly.

All the forms listed in the synonymy are similar to one another and differ from all other species of *Calamaria* having 5 supralabials and a preocular by their relatively high ventral counts (usually more than 175) and their thick, short, blunt tails. Since no two of the forms listed in the synonymy are sympatric, we are obliged in arriving at a decision to rely on experience with other unrelated sympatric species. The differences betweens pairs of these samples (Tables 48) are less than the differences that normally distinguish sympatric species of *Calamaria* (Table 1). The possibility remains that we are dealing here with an extreme case of the parallelism common in this genus (p. 257), and that several species are involved.

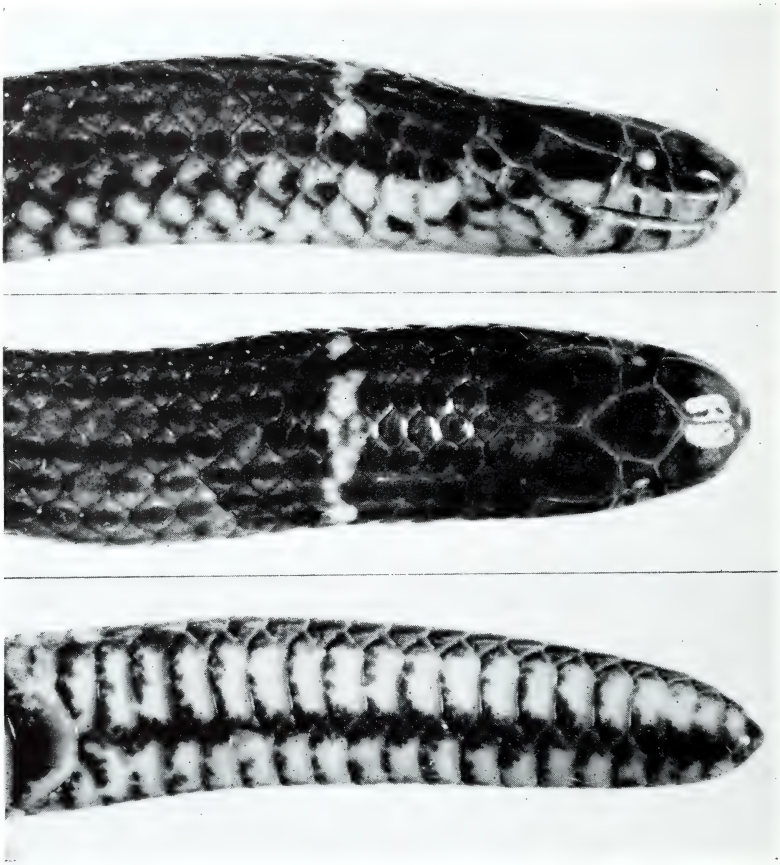

Fig. 52. Holotype of *Calamaria virgulata*.

The pattern of geographic variation in this wide ranging species is discussed in detail below.

Diagnosis.—Maxillary teeth modified, third and fourth supralabials entering orbit, preocular present.

If mental separated from chin shields and paraparietal surrounded by 6 scales, ventrals in males more than 185, in females more than 210.

If mental separated from chin shields and paraparietals surrounded by 5 scales, ventrals in males more than 175, females more than 179.

If mental touching chin shields and paraparietal surrounded by 6 scales, ventrals in males more than 159, in females more than 179.

Description.—Rostral wider than high, portion visible from above usually less than half of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 1¾ to 3½ times width of supraocular, about ⅔ to ¾ length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 or 6 shields and scales; nasal smaller than postocular; preocular present; neither ocular as high as eye; eye ⅔ to slightly more than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest, first, third and fourth subequal, second somewhat larger; mental triangular, separated from or touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.008–0.023 (17 specimens); tail thick, tapering abruptly at end to blunt tip; dorsal scales reduce to 4 rows on tail opposite first to ninth subcaudal anterior to terminal scute. Two specimens (holotype of *quinquetaeniata*, and NMS unnumbered) have 6 rows to the tip.

Hemipenis forked opposite third to fifth subcaudal; retractor muscle beginning opposite eighth subcaudal; calyces smooth (3 specimens). Cloaca of female bulbous (1) or bilobed (1).

Eight to 10 modified maxillary teeth (10 specimens).

Ventrals: males, 160–237 (mean 193.7; N=19); females, 180–260 (mean 215.1; N=39). Subcaudals: males, 16–30 (mean 19.3; N=20); females, 8–16 (mean 11.1; N=39).

Total length: males, 100–286 mm.; females, 131–374 mm. Ratio of tail to total length: males, 0.050–0.102 (mean 0.066; N=20); females, 0.022–0.055 (mean 0.034; N=39).

Color dark brown above, each scale with a light network, with or without longitudinal dark stripes; a yellow ring 1 to 3 scales wide on rear of head, or 4 to 8 scales behind head, or absent; dark longitudinal stripes between first and second scale rows, on third scale row, between fourth and fifth scale rows, and on sixth scale row; some specimens with stripes on third, fifth, and vertebral scale rows, some specimens without longitudinal stripes; an interrupted yellow ring present or absent at root of tail; usually a yellowish spot at tip of tail; head dark brown above and on sides, upper lip usually yellowish; underside of head yellowish, with or without brown spots; ventrals whitish to brownish black; dark pigment restricted to lateral corners of ventrals in some specimens; in others dark pigment extends across anterior margins of ventrals; in still others dark pigment

TABLE 48.—Geographic Variation in *Calamaria virgulata.*

		Ventrals		Subcaudals		Tail ratio[1]		Reduction to four dorsals[2]	
	No.	Range	Mean	Range	Mean	Range	Mean	Range	Mean
				MALES					
Java (*virgulata*)	3	189–197	194	17–20	18.7	59–67	64	2–3	2.7
Borneo (*brachyura*)	3	178–183	180.3	18(3)	..	70–74	73	4–8	6.7
Sulu	2	186–189	187.5	16–17	16.5	56–57	56	6–9	7.5
Mindanao:									
Southern Zamboanga (*zamboangensis*)	1	177	..	21	..	81	..	5	..
Northern Zamboanga + Cotabato (*mearnsi*)	2	227(1)	..	18–20	19	52–57	55	4–8	6
Celebes:									
Northern (*collaris*)	4	201–237	221.5	17–30	20.8	57–78	64	1–7	4.8
Central	2	160–170	165	19–22	20.5	82	..	6–7	6.5
Southern (*gracilis*)	1	190	..	18	..	63	..	7	..
				FEMALES					
Sumatra (*anceps*)	1	212	..	9	..	30	..	3	..
Borneo (*brachyura*)	6	194–205	201.3	9–16	11.0	28–55	36	1–5	3.0
Palawan	3	184–205	196	8–14	10.3	29–49	35	2–3	2.7
Sulu	3	197–201	199	11(3)	..	33–37	35	4–5	4.3
Mindanao:									
Southern Zamboanga (*zamboangensis*)	2	201(2)	..	12–13	12.5	44–45	44	4(1)	..
Cotabato (*mearnsi*)	2	235–247	241	12–13	12.5	39–40	39	5(2)	..
Celebes:									
Northern (*collaris*)	8	237–260	247.6	10–11	10.3	22–30	27	1–5	2.8
Central	5	180–194	186.0	10–11	10.2	32–36	34	2–5	3.6
Southern (*gracilis*)	7	208–240	215.6	10–13	11.9	29–43	38	0–5	4.0

[1] Ratio in thousandths of total length.

[2] Position in terms of subcaudals from terminal scute.

TABLE 49.—Frequency Distribution with Respect to Coloration in *Calamaria virgulata*.

	Dorsal stripes		Nuchal collar			Belly color		
	Present	Absent	On parietals	Behind parietals	Absent	White	Black and White	Black
Java	3	0	0	3	0	0	3	0
Sumatra	2	0	0	1	1	2	0	0
Borneo	9	0	0	9	0	9	0	0
Palawan	3	0	0	0	3	0	0	3
Sulu	0	5	0	0	5	2	0	3
Zamboanga	3	0	0	0	3	0	0	3
Cotabato	0	4	0	4	0	3	0	1
Celebes (north)	0	9	9	0	0	4	5	0
Celebes (center)	0	8	7	1	0	0	8	0
Celebes (south)	0	8	3*	0	5	0	8	0

* Two of these have interrupted light collars.

covers all except posterior edges of ventrals; underside of tail with same pattern as belly except that a median dark stripe is usually present (Table 49).

Geographic variation.—Tables 48 and 49 summarize the geographic variation observed. Only four varying characters are not shown in the tables. The three Javan specimens have a narrow dark vertebral stripe whereas those from Borneo and Palawan have stripes on the paravertebral scale rows. One Sumatran snake (ZMB 11436) has dark stripes on the paravertebral rows and a second (ZMA 10240) has a dark vertebral stripe.

The eye in the specimens from Cotabato Province, Mindanao and Java is distinctly smaller than the eye-mouth distance, whereas in other samples the eye is almost equal to, or slightly greater than the eye-mouth distance.

In specimens from Java and Celebes the paraparietal is surrounded by six shields and scales. In those from the Sulu Islands, Palawan, and Borneo the paraparietal is surrounded by five. Both counts are found in Sumatran snakes.

The populations from central and southern Celebes differ from all others in having the mental touching the anterior chin shields. Only in this character does the nominate form *gracilis* (southern Celebes) differ from all other populations of this species.

As shown in the tables, the several characters vary independently of one another. Any two samples picked at random from these

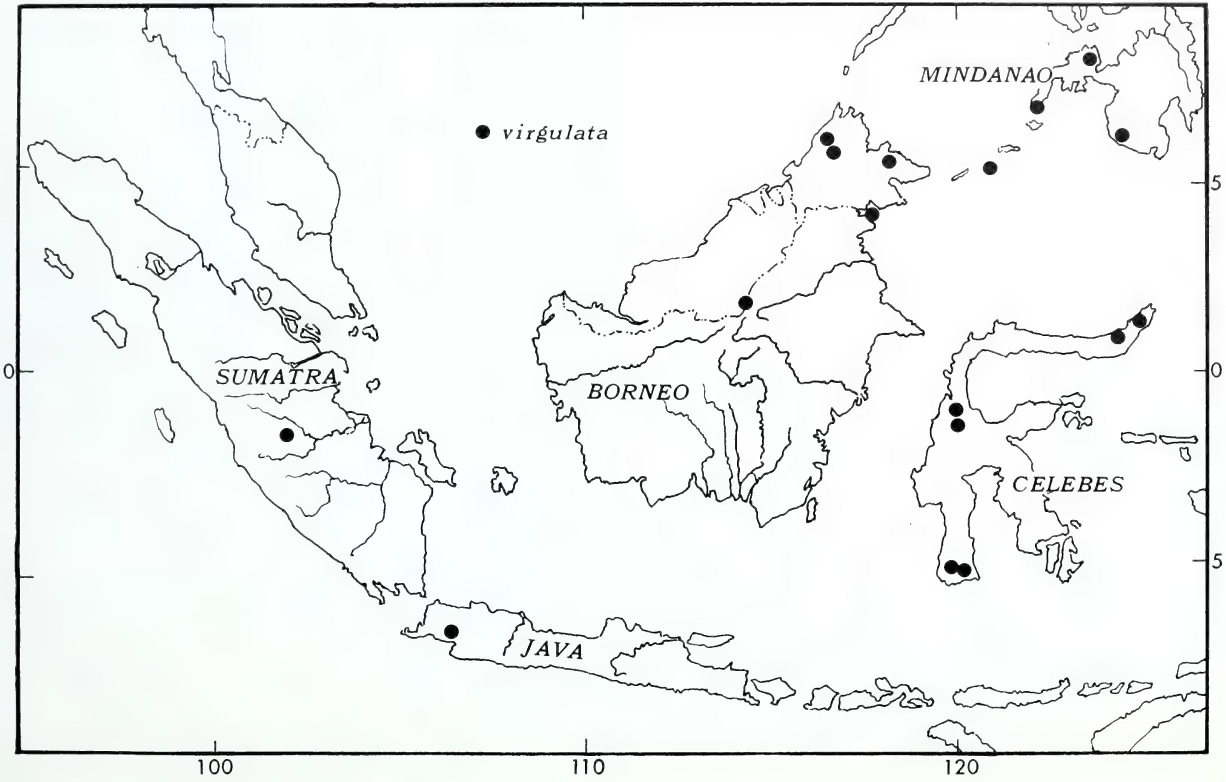

Fig. 53. Distribution of *Calamaria virgulata*.

tables differ in some characters. If only two samples were available, we could recognize them as taxonomically distinct. If a third sample were selected at random it would be intermediate. The character differences form a mosiac that prevents our recognition of these samples as distinct taxonomic entities. See the discussion under *lumbricoidea* (p. 85) for another example of the same phenomenon.

Ecological notes.—One specimen (CNHM 63571) was found under a log in a cut over forest in North Borneo. A second partially digested specimen, was removed from the stomach of a civet (*Viverra tangalunga*) collected at the same locality as the one above.

Distribution.—Sumatra, Borneo, Java, Celebes, and the southern Philippine Islands (Fig. 53).

SUMATRA (ZMB 11436—holotype of *anceps*). Goenoeng Sahilan (ZMA 10240).

JAVA (RMNH 39—holotype; NHMW 16695). Djawa Barat: Mount Salak (USNM 44118).

NORTH BORNEO. Mount Kina Balu (BM 95.11.7.26—holotype of *brachyura*). Kota Belud District: Mount Kina Balu, Kenokok River, 1000 meters (MCZ 43577–78), Mount Kina Balu, Saiap (BM 96.4.29.6–7). Ranau District: Mount Kina Balu, Luidan River, near Bundu Tuhan (MCZ 43579). Sandakan District: Sapagaya Forest Reserve (CNHM 63571).

INDONESIAN BORNEO. Nunukan Island (GM 3235); Mount Tibang (MCZ 22648—holotype of *egregia*).

SULU ARCHIPELAGO (NHMW unnumbered; MHNP 6133[4]).

MINDANAO. Zamboanga Province: Zamboanga (MCZ 15720; SU 13477—paratype of *zamboangensis*), Gumay area, 5–6 km. SE of Buena Suerte, west side of Dapitan Peak, about 760 meters (SU 22405). Cotabato Province: Saub (MCZ 25722–24), Tangob USNM 36911—holotype of *mearnsi*).

PALAWAN. Palawan Province: about 3–4 km. WNW of Iwahig, southeast slope of Thumb Peak, about 245 meters (SU 23167), about 2 km. SW of Iwahig, along bank of Malagau River, about 30 meters (SU 23168), 7–8 km. south of Bolicao, near the north end of the Village Range, about 60 meters (SU 23170).

Celebes (NHMW 16455). Bone Mountains, Tomohon (BM 96.12.9.68-72 —syntypes of *collaris;* NMB 1695-96—syntypes of *collaris;* SNG 19408; ZMH 4753); Bolaang-Mongondow (GM 3234); Manado (RMNH 40); Kulawi (GM 3231[4]); Kantewu (GM 3232[2]), between Kantewu and Peana (GM 3233), Bua Praeng (NHMW 16716:1-2; SNG 19441), Mount Bonthain, 1830 meters (BM 96.4. 29.37-38—syntypes of *gracilis*), south Celebes, 610 meters (BM 96. 4.29.36—syntype of *gracilis*), south Celebes (NMS 2 unnumbered).

East Indies (MCZ 7106—holotype of *albopunctata;* MHNP C2320 12.35—holotype of *quinquetaeniata*).

?New Guinea (MHNP 5780). We doubt the accuracy of the label; this is the only specimen of *Calamaria* supposedly from New Guinea. This snake almost certainly came from North Celebes, for it has the characters typical of the population from there, i.e., small eye, parietal collar, mental separated from the chin shields, and high ventral counts (female—236).

Specimens examined.—59.

Calamaria borneensis Bleeker. Figure 54.

Calamaria borneensis Bleeker, 1860, Nat. Tijds. Ned. Indië, **21**, p. 296—Sintang, Borneo; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 347, pl. 19, fig. 1; 1896, *ibid.*, **3**, p. 648; Bartlett, 1895, Sarawak Mus. Note Book, no. 1, p. 84; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 85; Barbour, 1912, Mem. Mus. Comp. Zool., **44**, p. 120; de Rooij, 1917, Rept. Indo-Austr., **2**, p. 175; Dunn, 1923, Jour. Malayan Branch Roy. Asiatic Soc., **1**, p. 2; Mertens, 1924, Zool. Anz., **60**, p. 159; Smith, 1925, Sarawak Mus. Jour., **3**, p. 4; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173; de Haas, 1950, Treubia, **20**, p. 564; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 200.

Holotype.—British Museum (Natural History) 1946.1.3.66.

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; preocular present; two pairs of infralabials touching anterior chin shields.

Description.—Rostral subconical, projecting, higher than wide, portion visible from above three-fourths length of prefrontal suture; prefrontal about four-fifths length of frontal, touching first 2 supralabials; frontal hexagonal, three-fourths length of parietal, 1¾ to 3 times width of supraocular (usually twice width); parietal 1½ times length of parietal; paraparietal surrounded by 6 shields and scales; nasal slightly smaller than postocular; preocular present, usually smaller than postocular, in a few specimens one-half size of postocular; neither ocular as high as eye; eye equal to or larger than eye-mouth distance; four supralabials, second and third entering eye, fourth longest, third half or less than half length of second, first slightly wider than third; mental triangular, touching anterior chin shields; 4 infralabials, first 2 touching anterior chin shields; second pair of chin shields meeting in midline; 3 or rarely 2, gulars between posterior chin shields and first ventral.

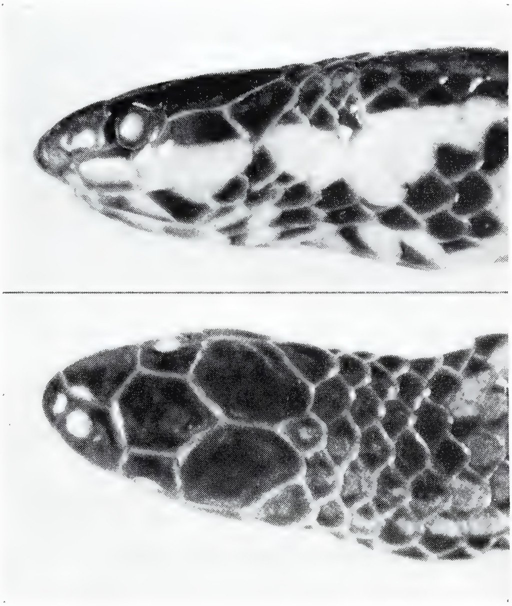

FIG. 54. *Calamaria borneensis* (CNHM 72372).

Body thickness index 0.013–0.031 (6 specimens); tail moderate, gradually tapered to point; dorsal scales reduced to 4 rows on tail opposite the second to eleventh subcaudal anterior to terminal scute.

Hemipenis not forked; retractor muscle beginning opposite sixth subcaudal; calyces papillate (2 specimens). Cloaca of female bilobed (1 specimen).

Eight or 9 modified maxillary teeth (7 specimens).

Ventrals: males, 126–169 (mean 155.0; N=24); females, 159–192 (mean 174.1; N=28). Subcaudals: males, 20–26 (mean 22.3; N=24); females, 13–21 (mean 18.2; N=28).

Total length: males, 135–355 mm.; females, 175–374 mm. Ratio of tail to total length: males, 0.087–0.133 (mean 0.103; N=22); females, 0.061–0.087 (mean 0.074; N=26).

Body dark grayish brown above, each scale pale with a fine dark reticulation; scattered dark spots or stripes on mid-dorsal scales; first scale row yellowish, occasionally crossed by dark bars; one to three yellow rings around tail, frequently interrupted mid-dorsally; yellow rings absent in a few specimens; head grayish brown above with indistinct darker spots; upper margins of supralabials dark brown; lower portions of supralabials yellowish with or without dark spots; underside of head yellowish with varying amounts of dark pigment or immaculate; ventral surface of body with a dark stripe along adjacent edges of ventrals and first scale row bordering a broad yellow stripe mid-ventrally, or with a bold checkered pattern or black and yellow; underside of tail checkered with black and yellow, the amount of dark pigment varying.

Geographic variation.—Local differentiation is evident in the color pattern. Six specimens from Long Mujan in the Baram River basin have dark transverse bars in the anterior third of the body; behind this point the bars are reduced to small spots. Four specimens from Nanga Padang, southwestern Borneo and two from western North Borneo have a series of small spots mid-dorsally, the length of each spot being less than twice its width. Seven specimens from Matang and Kuching (localities less than thirty miles apart) have very narrow dark stripes on adjacent borders of the fourth and fifth, and fifth and sixth scale rows. Four specimens from various localities in the Baram basin other than Long Mujan have small dorsal spots (3 specimens) or narrow longitudinal stripes (1). All the specimens from Long Mujan and one from Ulu Saoh (in Rejang basin) have a checkered ventral pattern. All of those from Nanga Pandang, Ma-

TABLE 50.—Comparison of Ventral and Subcaudal Counts in Bornean Samples of *Calamaria borneensis.*

		Ventrals		Subcaudals	
Localities	No.	Range	Mean	Range	Mean
			MALES		
Long Mujan.........	9	155–69	161.8	20–22	21.5
Baram...............	1	156	..	21	..
Kuching-Matang.....	4	152–55	153.0	22–24	23.0
Nanga Padang.......	2	153–58	155.5	23–25	24.0
			FEMALES		
Long Mujan.........	5	170–82	176.0	13–19	16.0
Baram..............	4	164–76	171.8	16–20	17.3
Kuching-Matang.....	5	171–92	178.6	16–20	18.6
Nanga Padang.......	2	171–72	172.5	20	..

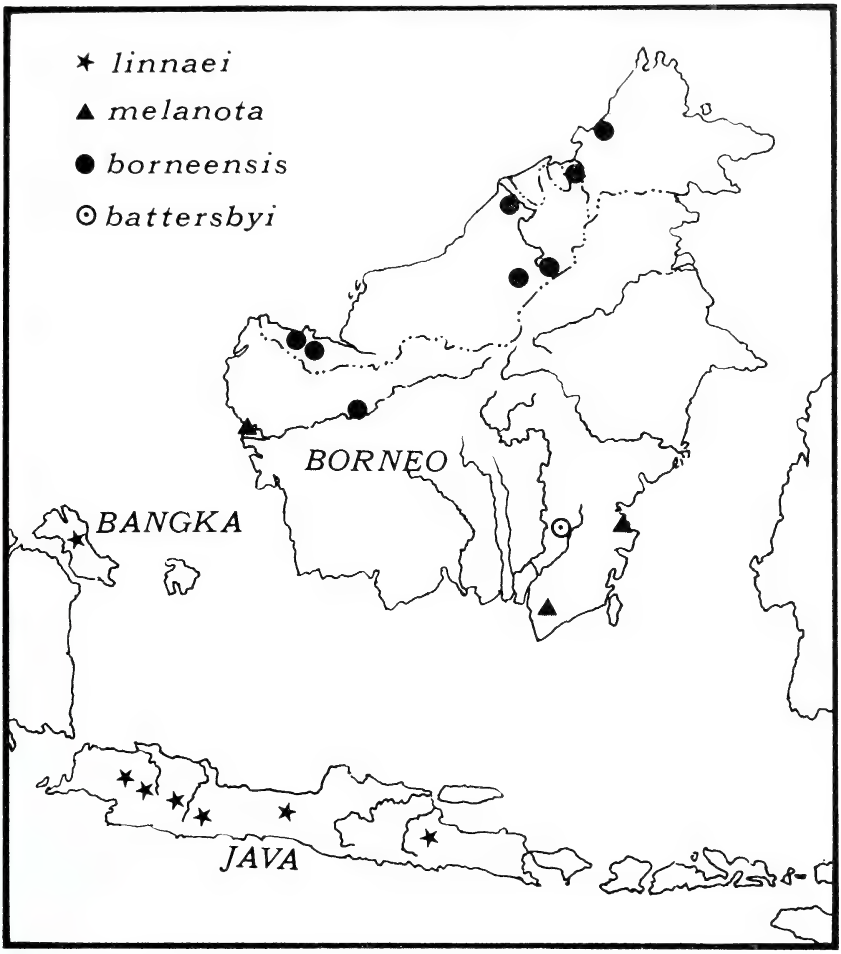

FIG. 55. Distribution of *Calamaria battersbyi*, *C. borneensis*, *C. linnaei*, and *C. melanota*.

tang, Kuching, and western North Borneo have a broad dark stripe on the lateral quarter of the ventrals. Two of the Baram specimens have ventral stripes and two a checkered pattern.

The ventral counts of males from Long Mujan are slightly higher than those of males from the Baram District, Kuching, Matang, and Nanga Padang. No local differentiation is evident in female counts or in subcaudal counts of males (Table 50).

Distribution.—Borneo (Fig. 55).

Sarawak (AMNH 63383; BM 95.2.28.29); north Sarawak (MCZ 11234–35). First Division: Kuching (BM 1933.6.20.26; NMS unnumbered; SM 5 unnumbered), 6 miles west of Kuching (CNHM 76296), Matang (BM 72.2.19.50–51). Third Division: Long Mujan (CNHM 72372; MCZ 16376–82; NMS 41, 48–49, 73, 75; SU 8569), Ulu Saoh (SM unnumbered). Fourth Division: Baram District (BM 97.3.4.6–7; MCZ 11263), Baram River (SNG 19435), Claudetown (BM 94.8.3.2), Kelabit Highlands (CNHM 109972; SM unnumbered). Fifth Division: Merapok (SM unnumbered).

North Borneo (NHMW 16178[4]); western North Borneo (SM 3 unnumbered). Papar District: Kimanis (CNHM 109973).

Indonesian Borneo: Sintang (BM 63.12.11.170—holotype), Nanga Padang (NHMW 16177[4]).

Borneo (AMNH 63384; USNM 49789; ZMB 8011; ZMH 4754); central Borneo (SMNS 4584[2]).

Specimens examined.—56.

Calamaria melanota Jan

Calamaria linnaei var. *melanota* Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 5—Borneo; 1865, Icon. Ophid., **10**, pl. 1, fig. 5.

Calamaria linnaei var. *gastrogramma* Jan, 1862, *loc. cit.*, p. 5—Borneo [Java *in error*]; 1865, *op. cit.*, pl. 1, fig. 4.

Calamaria benjaminsi Edeling, 1864, Ned. Tijds. Dierk., **2**, p. 202—Martapura, Borneo; Boettger, 1893, Mitt. Geogr. Ges. Nat. Mus. Lübeck, (2), **5**, p. 2; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 347; Bartlett, 1895, Sarawak Note Book, no. 1, p. 85; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 175; Mertens, 1924, Zool. Anz., **60**, p. 159; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173; de Haas, 1950, Treubia, **20**, p. 564; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 200.

Calamaria melanota, Boulenger, *op. cit.*, p. 349; Bartlett, *op. cit.*, p. 85; de Rooij, *op. cit.*, p. 177; Werner, *loc. cit.*, p. 174; de Haas, *loc. cit.*, p. 571 (part); Marx and Inger, *loc. cit.*, p. 204.

Calamaria electa Barbour, 1927, Proc. Biol. Soc. Washington, **40**, p. 128—Pasir, Borneo; de Haas, *loc. cit.*, p. 566; Marx and Inger, *loc. cit.*, p. 201.

Holotype.—Rijksmuseum van Natuurlijke Historie 37.

Taxonomic notes.—The holotype of *gastrogramma* is identical with that of *melanota* except that the color is slightly lighter. The pattern is identical. Although Jan (1862) gave the locality for *gastrogramma* as Java, the label with the holotype has the locality as Borneo, the collector as Schwaner, and the year as 1845. The Rijksmuseum has no Javan specimen corresponding to the figure of *gastrogramma* and antedating Jan's publication.

The original description of *benjaminsi* does not provide any means of distinguishing that form from *melanota.* The original description mentions the striking pattern of the ventrals (Fig. 56) so characteristic of *melanota.*

The original description of *electa* erroneously gave the supralabial count as 5; we examined the holotype which is identical with that of *melanota* and found only 4 supralabials.

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; preocular present; mental touching anterior chin shields; each ventral transversely divided into a dark anterior half and a light posterior half; tail tapered in posterior half.

Description.—Rostral usually higher than wide, portion visible from above equal to length of prefrontal suture; prefrontal shorter than frontal, touching first 2 supralabials; frontal hexagonal, 2 to 3⅓ times width of supraocular, about four-fifths length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular as high as postocular; neither ocular as high as eye; eye usually equal to eye-mouth distance; 4 supralabials, second and third entering eye, fourth longest, third half or less than half length of second, first longer than third; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shield; second pair of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.015–0.028 (5 specimens); tail moderate, tapering in posterior half to a point; dorsal scales reduce to 4 rows on tail opposite second to tenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth to sixth subcaudal; retractor muscle beginning opposite eighth or ninth subcaudal; calyces smooth (2 specimens).

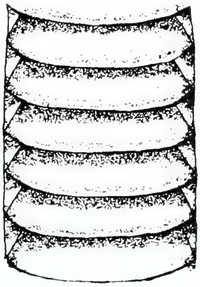

FIG. 56. Ventral pattern of *Calamaria melanota.*

Eight or 9 modified maxillary teeth (7 specimens).

Ventrals: males, 121–142 (mean 131.1; N=9); females, 131–154 (mean 143.3; N=9). Subcaudals: males, 23–26 (mean 24.3; N=9); females, 16–20 (mean 17.6; N=9).

Total length: males, 168–240 mm.; females, 185–260 mm. Ratio of tail to total length: males, 0.116–0.130 (mean 0.124; N=9); females, 0.074–0.087 (mean 0.081; N=9).

Body dark brown above; each scale with a light spot or light reticulation at tip; scales of first two or three rows with much larger light areas than those of rows above; head dark brown above; supralabials dark with yellow centers; underside of head yellowish with varying amounts of dark spots; each ventral transversely divided into a dark anterior and a light posterior half; subcaudals colored as ventrals.

Distribution.—Southern and southeastern Borneo (Fig. 55).

INDONESIAN BORNEO: Kuala Kapuas (NMB 12020), Martapura (holotype of *benjaminsi*—not examined), Pasir River (MCZ 22650—holotype of *electa*).

Borneo (NHMW 16176; NMB 1721; RMNH 31, 35—holotype of *gastrogramma*, 37—holotype; ZMB 8478; ZMH 5425; ZSBS 2039/0[2]); southeast Borneo (BM 84.9.13.1–3; CNHM 109964); central Borneo (SMNS 4529); west coast of Borneo (RMNH 1152).

Specimens examined.—17.

Calamaria linnaei H. Boie. Figures 12, 13.

Calamaria linnaei H. Boie *in* F. Boie, 1827, Isis, **20**, p. 539—Java; Schlegel, 1837, Phys. Serpens, pt. 2, p. 28, pl. 1, figs. 17, 18; 1837, Abbild. Amph., p. 15, pl. 4; Duméril and Bibron, 1854, Erp. Gèn., **7**, p. 63, pl. 64, figs. 1–4; Günther, 1858, Cat. Col. Snakes Brit. Mus., p. 3; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 6; Lidth de Jeude, 1890, Weber's Zool. Ergeb. Reise Nied. Ost-Ind., **2**, p. 182; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 345; 1897, Proc. Zool. Soc. London, **1897**, p. 225; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 85; Barbour, 1912, Mem. Mus. Comp. Zool., **44**, p. 119; Annandale, 1917, Jour. Fed. Malay States Mus., **7**, p. 107; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 174, fig. 67 (part); Dunn, 1927, Amer. Mus. Novit., no. 287, p. 3; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173 (part); Kopstein, 1930, Treubia, **11**, p. 303, fig. 8; *ibid.*, **12**, p. 274; 1932, *ibid.*, **14**, p. 79, fig. 4; 1938, Bull. Raffles Mus., no. 14, p. 129, pl. 21, figs. 45 and 46; Brongersma, 1931, Mem. Mus. Roy. Hist. Nat. Belg., (H.S.), **5**, no. 2, p. 35; de Witte, 1933, Bull. Mus. Roy. Hist. Nat. Belg., **9**, p. 5; de Haas, 1950, Treubia, **20**, p. 570 (part); Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 203; Hoesel, 1959, Ophidia Javanica, p. 24, fig. 17.

Calamaria multipunctata Reinwardt *in* F. Boie, *loc. cit.*, p. 540—Java; Kopstein, 1941, Temminckia, **6**, p. 134.

Calamaria maculosa Reinwardt *in* F. Boie, *loc. cit.*, p. 540—Java.

Calamaria reticulata Reinwardt *in* F. Boie, *ibid.*—Java.

Calamaria versicolor Ranzani, 1837, Mem. Soc. Ital. Modena, **21**, p. 113, pl. 3—Java; Duméril and Birbron, 1854, Erp. Gén., **7**, p. 69; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 6; 1865, Icon. Ophid., **10**, p. 1, fig. 7.

Calamaria linnaei var. *tessellata* Jan, 1862, *loc. cit.*, p. 5, pl. 5—Java; 1865, *op. cit.*, pl. 1, fig. 1.

Calamaria linnaei var. *bilineata* Jan, 1862, *loc. cit.*, p. 5—Java; 1865, *op. cit.*, pl. 1, fig. 2.

Calamaria linnaei var. *transversalis* Jan, 1862, *loc. cit.*, p. 5—Java; 1865, *op. cit.*, pl. 1, fig. 3; Boettger, 1894, Semon's Zool. Forsch. Austr., p. 123.

Calamaria linnaei var. *contaminata* Jan, 1862, *loc. cit.*, p. 5—no locality; 1865, *op. cit.*, pl. 1, fig. 6.

Calamaria versicolor var. *rhomboidea* Jan, 1862, *loc. cit.*, p. 5—Java; 1865, *op. cit.*, pl. 1, fig. 8.

Calamaria brevis Boulenger, 1894, *op. cit.*, p. 348, pl. 19, fig. 3—no locality; Werner, 1929, *loc. cit.*, p. 174; Marx and Inger, *loc. cit.*, p. 207 (addendum in reprint).

Calamaria sondaica Barbour, 1908, Bull. Mus. Comp. Zool., **51**, p. 319—Buitenzorg, Java; 1912, *loc. cit.*, p. 121; de Rooij, *loc. cit.*, p. 166; Werner, 1929, *loc. cit.*, p. 172; de Haas, *loc. cit.*, p. 574; Marx and Inger, *loc. cit.*, p. 206.

Calamaria linnaei var. *multilineata* Werner, 1909, Zool. Jahrb., (Syst.), **28**, p. 278—"Sumatra" [in error].

Calamaria borneensis var. *ventrimaculata* Holtzinger, 1916, Zool. Anz., **48**, p. 33—"Indonesia" ["Java" written on specimen label].

Calamaria margaritophora gastropicta Holtzinger, 1920, Arch. Naturg. Berlin, **85**, p. 106—Indonesia; Marx and Inger, *loc. cit.*, p. 204.

Calamaria pavimentata (non Duméril and Bibron), Holtzinger, 1920, *loc. cit.*, p. 108.

Changulia multipunctata, Mertens, 1929, Senckenbergia, **11**, p. 30; de Haas, 1941, Trebuia, **18**, p. 369.

Holotype.—Rijksmuseum van Natuurlijke Historie 27.

Taxonomic notes.—When H. Boie wrote his manuscript in Leiden prior to his departure for Java there were available to him four lots of *Calamaria* from Java. Three of these lots had already been assigned manuscript names by Reinwardt; they were *multipunctata* (RMNH 26), *maculosa* (RMNH 32), and *reticulata* (RMNH 29). The remaining specimen (RMNH 27), collected by Kuhl and van Hasselt, must have been the animal used by H. Boie for the diagnosis of the genus and listed by him as *Coluber calamarius* Linnaeus. This last specimen must therefore stand as the holotype of *Calamaria linnaei* H. Boie.

The holotype is a male; total length 243 mm., tail length 21 mm., ventrals 140, and subcaudals 19. The dorsal color pattern consists of transverse dark bands on a light background, as in the specimen in the center of the right hand row of Fig. 12. The ventral pattern is similar to that of the middle snake in the lower row in Fig. 13. The holotype also has modified maxillary teeth.

Two of the synonyms were based on variants in scutellation (*brevis* and *sondaica*). The only way in which the holotype of *brevis* differs from *linnaei* is in the meeting of the first infralabials behind the mental. However, this contact is extremely narrow and resembles that observed in a small proportion of specimens from definite localities on Java. In coloration and other elements of scutellation, the holotype of *brevis* is identical to *linnaei*.

The holotype of *sondaica* is identical to *linnaei* except for certain aspects of the head scutellation. The right side has five supralabials, but the line between the second and third appears to be the result of an injury. The left side has four supralabials as in *linnaei*. The first infralabials meet behind the mental. Otherwise the snake is a typical *linnaei*, having the characteristically thick body and one of the color patterns. We have seen many typical specimens of *linnaei* from Bogor (=Buitenzorg), the type locality of *sondaica;* three of 64 specimens from there have the first infralabials meeting behind the mental.

Holtzinger assigned the holotype of *gastropicta* to *margaritophora* but did not give the labial counts. This holotype, which we have seen, has four supralabials, the second and third entering the orbit, and therefore differs radically from the syntype of *margaritophora*, which we have also seen. In scutellation and coloration *gastropicta* falls in the range of variation of *linnaei*.

The variety *multilineata* Werner merely represents one of the common color patterns of *linnaei* found on Java. Werner (1909a) mistakenly assumed that these three specimens came from Sumatra. One of the paratypes (IRSNB 4313:22γ) from Pondok Gede, Java (6°17'S, 106°54'E) was collected on the same day by the collector of the holotype of *multilineata* (4313:336). Though we cannot find the type locality "Fjiloewar" in any gazeteer, the locality must be adjacent to that of the paratype. The third specimen (4008:336B) is just listed as from "Sumatra."

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; preocular present; mental touching anterior chin shields; three pairs of infralabials touching anterior chin shields;

ventrals spotted with black rectangular markings or, if not, lateral corners of successive scutes not identical in color.

Description.—Rostral higher than wide, portion visible from above equal to or slightly less than length of prefrontal suture; prefrontals shorter than frontal, touching first 2 supralabials; frontal hexagonal, 1⅓ to 2 times width of supraocular, equal to or slightly shorter than length of parietal; parietal longer than prefrontal; paraparietal surrounded by 6 scales and shields; nasal smaller than postocular; preocular present, as high as postocular, width one-half that of postocular; neither ocular as high as eye; diameter of eye equal to or slightly greater than eye-mouth distance; 4 supralabials, second and third touching eye, fourth longest; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; usually 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.008–0.100 (10 specimens); tail short, thick, tapering abruptly near end to blunt tip; dorsal scales reduce to 4 rows on tail opposite second to tenth subcaudal anterior to terminal scute or not reducing to four rows (4 specimens).

Hemipenis forked opposite fifth or sixth subcaudal; retractor muscle beginning opposite ninth subcaudal; calyces smooth (4 specimens). Cloaca of female bilobed (2 specimens).

Ten modified maxillary teeth (18 specimens).

Ventrals: males, 130–149 (mean 139.1; N=75); females, 148–166 (mean 154.8; N 95). Subcaudals: males, 15–22 (mean 17.7; N=74); females, 7–13 (mean 10.4; N=95).

Total length: males, 116–336 mm.; females, 91–396 mm. Ratio of tail to total length: males, 0.053–0.113 (mean 0.084; N=74); females, 0.029–0.054 (mean 0.042; N=94).

Ground color (Figs. 12, 13) black to light sandy brown; most dorsal scales light with a dark network; usually small isolated black spots scattered over the body; spots frequently unite to form more or less continuous black stripes occupying central portions of scales; most individuals with very thin light chevron immediately behind the head; one-third of individuals with continuous light stripe on adjacent halves of the second and third scale rows; about two-thirds of specimens have other scale rows very narrowly edged with white, forming a series of zigzag light lines; some snakes light sandy brown with dark diamonds or transverse bars mid-dorsally; a few specimens have two or three light triangles extending upward from ventral surface on to dorsal surface of tail; caudal triangles may reach across the tail leaving a series of dark diamonds between them.

Ventrals are whitish or cream colored with varying amounts of black pigment (Fig. 13). In some the dark pigment is restricted to the outer margins of the ventrals. From this extreme the specimens run the gamut from those with a few black squares on the lateral quarters or thirds of every third to fifth ventral through stages in which approximately every third to fifth ventral is half black or completely black giving a black checkered appearance. The underside of the tail may be uniformly cream-colored or have varying amounts of black. The amount of black may vary from a very small mid-ventral streak to a tail that is almost one-half black.

Individual variation.—One of 604 specimens lacks a preocular on one side of the head. Two others have two postoculars on one side of the head.

Four specimens have five supralabials on both sides of the head. In three of them the third and fourth labials of one side and second to fourth labials of the other enter the orbit. In the fourth specimen the third and fourth labials enter the orbit on both sides.

Five specimens have five supralabials on one side of the head and four on the other. Four of these snakes have the third and fourth labials entering the orbit on the side with five. The fifth specimen has the second to fourth labials entering the orbit on the side with five.

Eight of the snakes examined have the infralabials meeting behind the mental.

In one specimen (RMNH 8620) the entire dorsal surface is a uniform dark brown; ventrally this specimen is uniformly cream-colored without any dark spots on the ventrals. This snake is 44 mm. longer than the next longest specimen, which is also a female.

Geographic variation.—Moderate to large samples were available from six localities on Java (Fig. 55). Geographic variation shown in Table 51 reaches a statistically significant level in scale counts and in the ratio of tail length to total length. As the localities are arranged in the table in order from west to east, it is clear that simple geographic clines are not involved. Variation in relative tail length is related to variation in ventral and subcaudal counts as changes in those counts should reflect changes in body proportions. If the subcaudals increase in number without a corresponding increase in the number of ventrals, relative tail length should increase.

TABLE 51.—Geographic Variation in *Calamaria linnaei* from Six Localities on Java. (Localities are arranged in order from west to east).

		Ventrals		Subcaudals		Tail ratio[1]	
Localities	No.	Range	Mean	Range	Mean	Range	Mean
				MALES			
Bogor	18	135–43	139.6	15–18	16.6	70–91	79
Tjibodas	4	142–45	143.2	17–18	17.8	82–89	86
Tjikadjang	25	132–42	137.0	15–19	17.6	77–95	85
Wonosobo	12	134–46	138.0	17–22	18.9	82–113	92
Tengger	2	145–49	147.0	19–21	20.0	53–83	68
				FEMALES			
Bogor	19	150–58	154.4	7–10	8.6	30–42	36
Tjibodas	4	151–61	155.8	8–11	10.0	41–53	45
Bandung	5	150–59	153.0	9–11	10.0	29–45	37
Tjikadjang	25	149–59	153.0	8–12	10.4	32–50	41
Wonosobo	19	150–64	155.1	9–13	12.0	34–53	48
Tengger	5	159–66	163.2	11	11	39–46	43

[1] Ratio in thousandths of total length.

The position of the reduction to four dorsal scale rows also varies geographically (Table 52). The reduction takes place closer to the vent (that is, a larger number of subcaudals lies between the level of the reduction and the terminal scute) in snakes from Tjikadjang and Wonosobo.

Usually the second pair of chin shields meets in the midline and three gulars lie on the midline between the chin shields and the first ventral. Thirty of 135 snakes (22 per cent) examined for this character have a fourth gular separating the second chin shields. This variant appeared in 6 of 35 from Wonosobo, in 5 of 10 from Pengalengan, in 3 of 4 from Malang, in 9 of 50 from Tjikadjang, in 6 of 7 (the seventh damaged) from the Tengger Mountains, and 1 of 15 from "Java." It did not appear in 29 from Bogor, 6 from Bandung, 4 from Tjibodas, or 8 from Garut.

The geographic variation shown by *linnaei* is extremely local. Samples from successive localities differ slightly in the characters shown in the tables, but a clear pattern of macrogeographic differentiation does not appear.

The six Bangka specimens do not differ from the Javan series in any character.

Distribution.—Java and Bangka (Fig. 55).

JAVA (BM 47.7.23.14=1946.1.3.45—holotype of *brevis;* MCG 36559; MZUS 3 unnumbered; NHMW 16182; NMS unnumbered;

Table 52.—Geographic Variation in the Position of Reduction to Four Dorsal Scale Rows in *Calamaria linnaei*.

	Number of subcaudals between level of reduction and terminal scute									
	0	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
	Number of males									
Bogor				1	5	4	5	1	2	
Tjibodas				2	1	1				
Tjikadjang					6	3	6	1	4	5
Wonosobo				2		3			3	2
Tengger					1	1				
	Number of females									
Bogor		2	5	9	2					
Tjibodas		1		3						
Bandung	1		2	2						
Tjikadjang		1	1	7	7	7	1	1		
Wonosobo		2		4	6	3	2	2		
Tengger		2	1	2						

RMNH 27—holotype, 29—holotype of *reticulata*, 26[3]—syntypes of *multipunctata*, 32[2]—syntypes of *maculosa;* USNM 43422; UZMO unnumbered; ZMB 1550, 3757, 4067, 6935, 8757[3], 10260[4], 20531–32, 20678, 28045, 29676—holotype of *ventrimaculata*, 29677—holotype of *gastropicta*, 29688[2], 29694, 29697–98, 29704, 29707–09, 29711, 29726, 31503[3], 31719[2]; ZMH unnumbered; ZSBS 1932/0, 2652/0); east Java (USNM 56209). Djawa Barat: Bogor (CNHM 83077–78; MCZ 7102—holotype of *sondaica*, 7519, 7524[3]; RMNH 14 unnumbered; USNM 43399–400, 43417–21, 43437, 43442–43, 43448–52, 43459, 43463–65, 43475, 43510, 43512–16, 43523, 120812), Bogor Botanical Gardens (RMNH 2 unnumbered), Bogor, Estate Tjomas (RMNH 6 unnumbered), vicinity of Bogor (RMNH 7 unnumbered), Gadok (CNHM 100870; UMMZ 80486), Bandung (NMS 4 unnumbered), Bandung, Lembang, ±1200 meters (RMNH unnumbered), ?Bandung (RMNH unnumbered), Pengalengan (SMNS 3091, 3478[2], 3475[7]), Sindanglaja (MCZ 7520), Mount Gede, Tjibodas (AMNH 31942–43; NMS unnumbered; RMNH 4 unnumbered USNM 62630), Mount Garut (RMNH 7 unnumbered), Mount Garut, plantation Dajeuhmanggoeng, ±1300 meters (RMNH unnumbered), Tjikadjang, 900 meters (RMNH 437 unnumbered), Tjiboeloe, near Tjikadjang, ±1500 meters (RMNH unnumbered), Palabuhan Ratu (USNM 62624), Mount Salak, Geoneong Boender (USNM 43453, 44064). Djawa Tengah: vicinity of Wonosobo, 700–1000 meters (RMNH 10 unnumbered), Wonosobo, Tlogodjati, ±1000

meters (RMNH 8620), Wonosobo, Modjotengah, ±1100 meters (RMNH 12 unnumbered), Wonosobo, Djetis, Sapoeran, ±600 meters (RMNH 9 unnumbered). Djawa Timur: Tengger Mountains, Nongkodjadiar, ±1200 meters (RMNH 7 unnumbered), Malang (RMNH 3922, 3 unnumbered).

BANGKA (ZMB 4539[3], 4540, 4541[2]).

?Borneo: Muara Tewe (AMNH 71508). This snake was part of a purchased collection that included a specimen of *Acanthophis antarcticus* (AMNH 71509) from the same locality. This last specimen is certainly mislabeled, for the genus *Acanthophis* is restricted to the Australian region. We doubt the accuracy of the locality of the American Museum specimen of *linnaei* because of its association with the obviously incorrectly labeled *Acanthophis*. De Rooij (1917) lists Borneo in the range of *linnaei*. Having examined all of the *Calamaria* material from Borneo in all museum collections without having found any *bona fide* Bornean *linnaei*, we are forced to conclude that the species does not occur in Borneo.

?Celebes: Manado (BM 71.7.20.206). This specimen, collected by A. B. Meyer (Boulenger, 1894, p. 346) is unquestionably *linnaei*, but the locality is very doubtful. In the first place, Meyer is the only man reported to have collected this common Javanese species in Celebes despite the relatively large numbers of *Calamaria* obtained from Celebes since his time (e.g., by the Sarasins, Everett, and Smith). Secondly, Meyer's "Manado" collection also included three other common Javanese snakes no one else has found in Celebes: *Calamaria modesta, Natrix subminiata,* and *N. vittata*. De Haas (1950, p. 544) and van Steenis-Kruseman (1950, p. 359) commented on the unreliability of Meyer's locality labels. We do not include Celebes in the range of *C. linnaei*.

?Sumatra (IRSNB 4008:336B—paratype of *multilineata*); Pondok-Gede (IRSNB 4313:22γ—paratype of *multilineata*); Fjiloewar (IRSNB 4313:336—holotype of *multilineata*). As noted above, these specimens are almost certainly from Java.

?Singapore (ZMH 8 unnumbered). These specimens of *linnaei* supposedly from Singapore were collected by W. Schwinghammer in 1909. This is the only sample reputedly from Singapore, which for many years has been an important animal market and entrepot. That in an area so well collected as Singapore Island no other specimen of this common Javanese form has ever been found, makes us doubt the validity of this locality.

No locality (RMNH 51–52, 79, 100).

Specimens examined.—659.

Calamaria battersbyi new species

Calamaria melanota (part), Boulenger, 1896, Cat. Snakes Brit. Mus., **3**, p. 648; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 177.

Holotype.—British Museum (Natural History) 96.2.17.13, a male from Tandjong, southeastern Borneo.

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; preocular present; mental touching anterior chin shields; each ventral with a dark anterior half and a light posterior half; narrow longitudinal stripes mid-dorsally; tail short, abruptly tapered at end.

Description of holotype.—Rostral broader than high, portion visible from above one-third length of prefrontal suture; prefrontal equal in length to frontal, touching first 2 supralabials; frontal hexagonal, 1⅔ width of supraocular, three-fourths length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; preocular as high as postocular but not as wide; neither ocular as high as eye; eye larger than eye-mouth distance; 4 supralabials; second and third touching eye, fourth longest, third half width of second, first almost equal to second; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Tail short, thick, tapering abruptly at end; dorsal scales reduce to 4 rows on tail opposite fourth subcaudal anterior to terminal scute.

Eight modified maxillary teeth.

Ventrals 171; subcaudals 16; total length 92 mm.; ratio of tail to total length 0.065; ratio of head width to total length 0.025, ratio of head length 0.048.

Body brown above; dorsal scales yellowish with brown margins; a thin dark stripe on adjacent edges of first and second scale rows; a slightly wider dark stripe on adjacent thirds of second and third rows; a similar dark stripe on adjacent halves of fourth and fifth rows; a narrow dark stripe along adjacent edges of sixth and vertebral rows; in posterior two-thirds of body a faint dark stripe along adjacent edges of ventrals and first scale row; thus anteriorly there are eight dark stripes and posteriorly ten; a narrow yellow ring around body seven scales behind head; a similar yellow ring around root of tail and an interrupted one around center of tail; head brown above and on sides to lip; lower half of fourth supralabial yellow; a narrow yellow streak in center of second and third supralabials; underside of head yellowish with brown spots; each ventral with dark stippling across anterior half, posterior half yellow; underside of tail with a dark streak in midline.

Comparisons.—This species differs from *melanota* in the shape and relative size of the tail, in dorsal coloration, in the relative sizes of supralabials, and in ventral and subcaudal counts of males.

The shape of the tail is similar to that of *linnaei*. But *battersbyi* differs from *linnaei* in ventral counts and coloration despite the extensive variation in coloration observed in *linnaei*.

Distribution.—Southeastern Borneo (Fig. 55).

Calamaria javanica Boulenger. Figure 57.

Calamaria javanica Boulenger, 1891, Ann. Mag. Nat. Hist., (6), **7**, p. 279—Java; 1894, Cat. Snakes Brit. Mus., **2**, p. 347, pl. 19, fig. 2; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 176 (part); Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173 (part); Brongersma, 1930, Treubia, **12**, p. 302 (part).

Calamaria javanica javanica, de Haas, 1950, Treubia, **20**, p. 568 (part); Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 202.

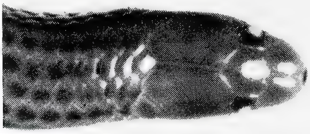

FIG. 57. *Calamaria javanica* (CNHM 109791).

Holotype.—British Museum (Natural History) 73.5.3.21.

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; no preocular; second pair of chin shields not meeting in midline.

Description.—Rostral higher than wide, portion visible from above one-third to two-thirds length of prefrontal suture; prefrontal slightly shorter than frontal, touching first 2 supralabials; frontal two to three times width of supraocular, about two-thirds length of parietal; parietal almost twice as long as prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; no preocular; postocular not as deep as eye; eye equal to eye-mouth distance; 4 supralabials, second and third touching eye, fourth longest, third not more than one-half length of second, first slightly larger than third; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields widely separated; 4 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.012 (1 specimen); tail short, gradually tapering to a blunt tip; dorsal scales reduce to 4 rows on tail opposite the third to eighth subcaudal anterior to terminal scute.

Eight to 9 modified maxillary teeth (2 specimens).

Ventrals: male, 176; females, 168–170 (mean 169.0; N=3). Subcaudals: male, 16; females, 10–12 (mean 11.0; N=3).

Total length: male, 186 mm.; females, 85–192 mm. Ratio of tail to total length: male, 0.065; females, 0.041–0.059 (mean 0.047; N=3).

Body dark brown above, each dorsal scale with small yellow specks; a narrow yellow vertical arc on each side about 6 scales be-

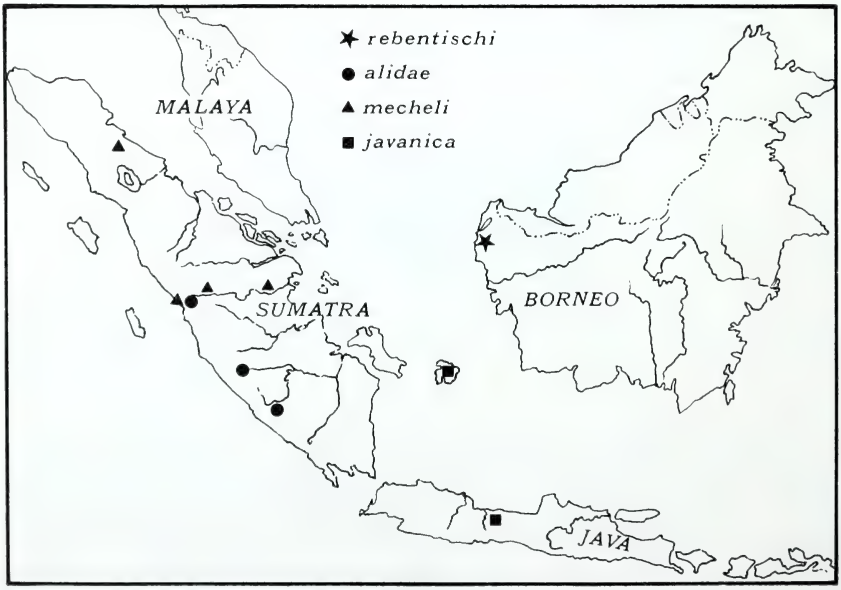

FIG. 58. Distributions of *Calamaria alidae*, *C. javanica*, *C. mecheli*, and *C. rebentischi*. No precise locality in Java.

hind head in holotype only; scales of first and second rows yellowish with small dark spot, the dark area increasing in the posterior half of the body; a small yellow vertical bar on each side at the root of the tail; head dark brown above and on upper edges of supralabials; rest of supralabials and underside of head yellow; ventrals yellow; behind anterior quarter of body a small brown spot at the lateral corners of each ventral; underside of tail yellow with dark brown midline and lateral quarters.

Distribution.—Java and Billiton (Fig. 58).

JAVA (BM 73.5.3.21—holotype).

BILLITON (CNHM 109791; ZMA 10075[2]).

De Rooij (1917) lists a locality on Sumatra. We have been unable to locate any Sumatran specimens of *javanica* in the collections of European or American museums.

Specimens examined.—4.

Calamaria buchi Marx and Inger. Figure 1.

Calamaria buchi Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 195, fig. 26—Dalat, Viet Nam, Indo-China.

Holotype.—Chicago Natural History Museum 71697.

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; preocular present; mental touching anterior chin shields; length of parietal greater than distance from posterior tip of frontal to posterior tip of rostral.

Description.—Rostral higher than wide, portion visible from above more than one-half length of prefrontal suture; prefrontal equal to or slightly shorter than length of frontal, touching first 2 supralabials, entering orbit at a point in holotype; frontal twice width of supraocular, about half length of parietal; parietal twice length of prefrontal, greater than distance from rostral to posterior tip of frontal; paraparietal surrounded by 5 shields and scales; nasal equal to or larger than both oculars; preocular larger or slightly smaller than postocular; neither ocular as high as eye; eye equal to or less than eye-mouth distance; 4 supralabials, second and third entering orbit, fourth longest, third two-thirds length of second, first slightly shorter than second; mental triangular, touching anterior chin shields; 5 infralabials, first 3 pairs touching anterior chin shields; second pair of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventrals.

Body thickness index 0.021 (1 specimen); tail short, slightly tapered, ending in obtuse point; dorsal scales reduce to 4 rows on tail opposite the third to fourth subcaudal anterior to terminal scute.

Nine modified maxillary teeth (2 specimens).

Ventrals: females, 221–236 (N=2). Subcaudals: females, 13–14.

Total length: females, 389–466 mm. Ratio of tail to total length: females, 0.039–0.041.

Color blackish above, each scale with small light spots; first scale row yellowish throughout length of body; second scale row yellowish in anterior part of body; head dark above; lower two-thirds of supralabials yellowish; underside of head yellowish immaculate except for a few very small scattered dark spots; ventrals yellow, immaculate; underside of tail yellowish with scattered dark spots; one specimen with two pairs of light spots on side of tail.

Distribution.—Southern Annam (Fig. 74).

INDO-CHINA. Annam: Dalat (CNHM 71697—holotype), Blao (USNM 90381).

Calamaria pavimentata Duméril and Bibron

Calamaria pavimentata Duméril and Bibron, 1854, Erp. Gén., **7**, p. 71—Java [in error]; Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 7; 1865, Icon. Ophid., **10**, pl. 1, fig. 9; Boulenger, 1890, Fauna Brit. India, Rept., p. 282; 1894, Cat. Snakes Brit. Mus., **2**, p. 348; 1903, Fasc. Malay. Zool., **1**, p. 175; 1909, Ann. Mag. Nat. Hist., (8), **4**, p. 495; 1912, Fauna Malay Penin., Rept., p. 157; Flower, 1896, Proc. Zool. Soc. London, **1896**, p. 886; 1899, *ibid.*, **1899**, p. 675; Cardow, 1896, Jour. Bombay Nat. Hist. Soc., **10**, p. 587; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 85; Laidlaw, 1901, Proc. Zool. Soc. London, **1901**, p. 577; Wall, 1903, Proc. Zool. Soc. London, **1903**, p. 93; 1919, Jour. Bombay Nat. Hist. Soc., **26**, p. 866; Mocquard, 1907, Rev. Colon., **1906**, p. 45; Steindachner, 1914, Denks. Akad. Wiss. Wien, **90**, p. 341; Smith, 1915, Jour. Nat. Hist. Soc. Siam, **1**, p. 213; 1922, Jour. Fed. Malay States Mus., **10**, p. 267; 1930, Bull. Raffles Mus., no. 3, p. 59; 1943, Fauna Brit. India, Rept., **3**, p. 238, fig. 83; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 176 (part); Procter, 1919, Jour. Bombay Nat. Hist. Soc., **26**, p. 184; Vogt, 1922, Arch. Naturg. Berlin, **88**, p. 141; Mell, 1922, *ibid.*, **88**, p. 122; 1929, Beit. Fauna Sinica, p. 10; 1929, Lingnan Sci. Jour., **8**, p. 212; Bourret, 1927, Invent. Gen. Indo-China, **3**, p. 234; 1934, Bull. Instr. Pub., **Apl. 1934**, p. 157; 1936, Serp. Indochine, p. 270, fig. 107; Angel, 1929, Bull. Mus. Nat. Hist. Nat., (2), **1**, p. 76; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 174 (part); Gee, 1930, Bull. Dept. Biol. Yenching Univ., **1**, p. 67; Fan, 1931, Bull. Dept. Biol. Sun Yat Sen Univ., no. 11, p. 105; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 193; Taylor and Elbel, 1958, Univ. Kansas Sci. Bull., **38**, p. 1044.

Calamaria quadrimaculata Duméril and Bibron, 1854, Erp. Gén., **7**, p. 73—Java [in error]; Jan, 1862, *loc. cit.*, p. 7; 1865, *op. cit.*, **10**, pl. 1, fig. 10; Günther, 1858, Cat. Colubrine Snakes, p. 4 (part); 1864, Rept. Brit. India, p. 197; 1892, List Rept. Fishes, *in* Pratt, Snow of Tibet, p. 239; Nicholson, 1874, Indian Snakes, p. 57.

Calamaria siamensis Günther, 1864, Rept. Brit. India, p. 196, pl. 18, fig. B—Siam and Cochin China; Nicholson, *op. cit.*, p. 57; Theobald, 1876, Desc. Cat. Rept. Brit. India, p. 140; Boettger, 1885, Ber. Offenb. Ver. Nat., **24** and **25**, p. 121; 1888, *ibid*, **26–28**, p. 128.

Calamaria berezowskii Günther, 1896, Ann. Mus. Zool. Acad. Sci. St. Petersburg, **1**, p. 205, pl. 1, fig. A—Lungan, Szechwan, China; Wall, 1903, *loc. cit.*, p. 93; Stejneger, 1907, Bull. U. S. Nat. Mus., **58**, p. 376, fig. 312; 1910, Proc. U. S. Nat. Mus., **36**, p. 107; Mell, 1929, Lingnan Sci. Jour., **8**, p. 212.

Calamaria pfefferi Stejneger, 1901, Proc. Biol. Soc. Washington, **14**, p. 191—Miyako Island, Riu Kiu Islands; 1907, *loc. cit.*, p. 378, figs. 313–316; Werner, 1929, *loc. cit.*, p. 174; Okada, 1927, Nihon Dobutsu Zukan, p. 207, fig. 400; Takahashi, 1930, Snakes Japan, Sp. No. 42; Maki, 1931, Monog. Snakes Japan, p. 138, pl. 51B, text fig. 92; Marx and Inger, *loc. cit.*, p. 205.

Calamaria pavimentata var. *uniformis* Smith, 1921, Proc. Zool. Soc. London, **1921**, p. 426—Langbian Peaks, Annam.

Calamaria pavimentata formosana Maki, 1931, Monog. Snakes Japan, p. 136, pl. 51, fig. A, text figs. 90–91—Arisan, Formosa; Marx and Inger, *loc. cit.*, p. 205.

Calamaria pavimentata banaensis Bourret, 1934, Bull. Gen. Instrut. Publ., no. 9, p. 10—Bana, Annam.

Calamaria pavimentata annamensis Bourret, 1937, Bull. Gen. Instrut. Publ., no. 13, p. 32—Dong Tam-ve, Prov. Quangtri, Annam; *ibid.*, no. 15, p. 77.

Calamaria pavimentata pavimentata, Pope, 1935, Rept. China, p. 305, pl. 12, figs. H, I, J; Bourret, 1935, Bull. Gen. Instrut. Publ., no. 10, p. 8; 1937, *ibid.*, no. 17, p. 22; *ibid.*, no. 18, p. 27; 1941, *ibid.*, no. 21, p. 14; 1943, *ibid.*, no. 24, p. 11.

Calamaria uniformis, Smith, 1943, Fauna Brit. India, Rept., **3**, p. 238; Marx and Inger, *loc. cit.*, p. 206.

Holotype.—Museum National d'Histoire Naturelle Paris 3298.

Taxonomic notes.—After examining the holotypes of *pavimentata* and *quadrimaculata*, we agree with the long established usage (Boulenger, 1894; Smith, 1943) of associating these names with the widely distributed species of southeastern Asia. In view of the extensive collecting that has been carried out in Java, *pavimentata* would certainly have been rediscovered in Java if it really occurred there.

The color pattern of this species is variable though it usually includes narrow, dark, longitudinal stripes. Most specimens have a broad black collar followed by a narrow yellow ring, which may be interrupted, and a pair of yellow bars at the root of the tail. Some or all of these pattern elements may be lacking. These variants appear over most of the species range, and some have been recognized as distinct species or subspecies, as for example, *pfefferi, formosana, banaensis*, and *uniformis*. To recognize any of these forms would be to place too much weight on characters showing much individual variation (as in *banaensis*) or recognizing subspecies on the basis of a single character (*formosana*).

Smith (1943) noted that the hemipenis in specimens from southern Annam (types of *uniformis*) were shallowly forked in contrast to the deep bifurcation in other *pavimentata*. We have observed similar intraspecific local differentiation in *lumbricoidea* (Inger and Marx, 1962).

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; preocular present; three pairs of infralabials touching anterior chin shields; all ventrals yellow with dark lateral tips; tail not as thick as body, tapering to sharp point.

Description.—Rostral as broad as high, or slightly higher than broad, portion visible from above one-half to equal to entire length of prefrontal suture; prefrontal equal to or shorter than length of frontal, touching first 2 labials; frontal hexagonal, 1⅔ to 3 times width of supraocular, about two-thirds length of parietal; parietal 1⅓ to 1½ times length of prefrontal; paraparietal surrounded by 5 or 6 shields and scales; nasal equal to or smaller than postocular; preocular usually larger than postocular; neither ocular as high as eye; eye usually larger than eye-mouth distance; 4 supralabials, second and third entering orbit, fourth largest, third slightly more than half length of second, first slightly smaller than second; mental triangular, usually separated from anterior chin shields by first infralabials; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting in midline; 3 gulars in midline between second chin shields and first ventrals.

Body thickness index 0.011–0.012 (2 specimens); tail moderately long, tapering gradually to a point; dorsal scales reduce to 4 rows on tail opposite first to thirteenth subcaudal anterior to terminal scute, or 5 rows to terminal scute (4 specimens).

Hemipenis forked opposite fifth subcaudal; retractor muscle beginning opposite seventh (Smith, 1943) to tenth subcaudal; calyces smooth (1 specimen).

Eight to 10 modified maxillary teeth (9 specimens).

Ventrals: males, 125–168 (mean 154.1; N=37); females, 137–206 (mean 170.9; N=50). Subcaudals: males, 13–33 (mean 22.3; N=38); females, 8–20 (mean 15.2; N=50).

Total length: males, 84–313 mm.; females, 115–485 mm. Ratio of tail to total length: males, 0.069–0.169 (mean 0.096; N=35); females, 0.037–0.085 (mean 0.058; N=48).

Color brownish; scales of upper rows usually with a brown network; usually narrow, dark, longitudinal lines, most often on adjacent edges of ventrals and first scale row, of first and second rows, of second and third rows, and of fourth and fifth rows; often a dark line down the center of the vertebral scales; usually a solid black collar 3 to 6 scales wide immediately behind head, collar sometimes limited to a black-edged area; dark collar followed by a complete or interrupted narrow yellow ring; usually a pair of vertical yellow bars at root of tail, the bars sometimes meeting and forming a complete ring; similar yellowish spots at tip of tail; head brownish above with indistinct darker markings; varying amount of dark pigment on supralabials, the lip always remaining yellowish; underside of head yellowish with varying amounts of dark pigment; ventrals usually yellowish except at outer tips (for variation see below); underside of tail with or without a dark median streak.

TABLE 53.—Geographic Variation in Color Pattern of *Calamaria pavimentata.*

	Mainland	*Insular*
Yellow collar		
complete	28	1
interrupted	6	21
absent	5	11
Black collar		
solid	30	17
margin only	3	3
absent	1	13
Yellow caudal ring		
complete	5	0
interrupted	24	0
absent	11	33

Individual variation.—Within a given population the yellow ring on the neck may be interrupted, complete, or absent. The ring is one to three scales wide. Our Formosan sample includes 10 lacking the yellow ring, 21 in which the ring is interrupted, and one in which the ring is complete.

TABLE 54.—Variation in Counts and Relative Tail Length in *Calamaria pavimentata*.

		Ventrals		Subcaudals		Tail ratio[1]	
Regions	No.	Range	Mean	Range	Mean	Range	Mean
				MALES			
Malaya	3	127–34	130.7	14–22	18.0	69–114	96
Cochin-China	2	125–58	141.5	20–30	25.0	90–131	111
Northern Annam	2	159–60	159.5	20–21	20.5	76–94	85
Southern Annam	3	146–49	147.3	31–33	32.0	122–169	148
Laos	2	154–56	155.0	20–22	21.0	86–87	86
Tonkin	4	158–68	164.8	18–19	18.8	69–82	76
Thailand	3	133–68	156.0	13–20	17.3	73–79	76
Burma	2	160–68	164.0	21–24	22.5	87–93	90
Formosa	13	148–66	158.8	20–25	22.8	84–103	94
				FEMALES			
Malaya	7	140–72	151.7	8–13	10.0	37–57	46
Cambodia	1	182	..	15	..	42	..
Northern Annam	2	181–206	193.5	14–15	14.5	49–57	53
Southern Annam	2	167–69	168.0	20	..	75–85	80
Laos	2	177–79	178.0	12–15	13.5	33–53	43
Tonkin	5	176–97	186.6	13–16	15.0	47–56	50
Burma	1	186	..	12	..	41	..
India	1	142	..	12	..	54	..
Szechwan	2	160–71	165.5	12–16	14.0	51–64	58
Formosa	24	166–85	174.5	16–18	17.1	57–70	65
Riu Kiu	1	162	..	13	..	49	..

[1] Ratio in thousandths of total length.

Similar variation is shown in the yellow caudal ring. Of nine specimens from Malaya, seven have a pair of yellow bars on the tail separated mid-dorsally, one has a complete yellow ring, and one has no yellow markings.

Most specimens seen have yellowish bellies except for a dark spot at the extreme outer edge of each ventral. In some specimens small brownish dots are scattered down the center of the belly; this variant appears in the Riu Kiu Islands, Tonkin, Laos, and Cochin-China; the samples from the last three Indo-Chinese areas also include specimens with unmarked ventral scales.

The black nuchal collar is present in only 17 of the Formosan specimens. This collar, though usually present, is poorly defined in one specimen each from Tonkin, Annam, and Burma, and is totally absent in one from Cambodia.

The four specimens in which the dorsal scale rows are not reduced to four are from Szechwan (2), Riu Kiu Islands, and Laos; they nonetheless show the tapered, pointed tail characteristic of *pavimentata*.

Geographic variation.—The island populations of Formosa and the Riu Kius have a higher frequency of certain pattern elements than the mainland samples (Table 53). *Calamaria formosana* and *C. pfefferi* are based upon these elements of pattern. We are not recognizing these insular forms because the same color variants are found with some frequency on the mainland, and because no other characters support the differentiation in coloration.

All Annam snakes (including types of *uniformis, banaensis,* and *annamensis*), whether from north or south Annam, lack the yellow caudal marking. Only three other specimens from scattered localities on the mainland lack this marking. The Annam samples are the only ones including specimens (4) having a dark mid-ventral stripe. Four of the five mainland specimens lacking the yellow collar are from Annam. Despite the fact that three names were applied to the Annam populations, we are not recognizing any subspecies from this area as only one character is truly diagnostic.

The southern Annam population (*uniformis*) has slightly higher subcaudal counts; males have 30 to 33 subcaudals as compared to 20–21 in males from farther north in Annam and 20–30 in males from Cochin-China. This character simply illustrates the common local differentiation of ventral and subcaudal counts found in many species of this genus. The extent of local differentiation in ventrals, subcaudals, and relative tail length is shown in Table 54.

All four specimens from Laos and one of nine from Tonkin have the mental touching the chin shields. In no other respect are these specimens distinguished from other Indo-Chinese *pavimentata.*

Distribution.—From western Burma, western Szechwan, eastern China, Formosa, and the Riu Kiu Islands, southward through the Malayan Peninsula (Fig. 74).

RIU KIU ISLANDS. Miyako (CAS 22062).

FORMOSA. Kanishirei (CAS 18878–79), Kosempo (BM 109.10. 29.7–8; CAS 18876–77; NHMW 16180[11]), Suisharyo (NHMW 16181[14]), Taihorin (NHMW 16179[4]), Wu She (CNHM 96623), Yang Ming Shan, Shan Tsu Hou (CNHM 131937).

CHINA. Kwangtung: Canton (SNG 19436). Szechwan: Mount Omei, Si Gi Pin (USNM 95452), Mupin (USNM 82655).

BURMA. Northern Chin Hills (BM 93.11.17.3), Pegu (BM 68.4. 38[2]).

THAILAND (MHNP 483). Hup Bon (BM 1938.8.7.50), Lam Tong Lang (USNM 101291).

INDO-CHINA. Laos: Xieng-Khouang (MHNP 28–50, 28–51, 28–52[2]). Tonkin (MHNP 37–33): Chapa (MHNP 38–141), Lao Kay (MHNP 08–191), Nga-Hai (NMB 7504), Pointe Pagode (MHNP 11–45), Tam Dao (CNHM 100869; MHNP 08–7, 35–2, 35–3). Annam: Bana (CNHM 11528; MHNP 38–140, C232348.91—holotype of *banaensis*), Dong Tam-Ve (MHNP C2323/17 58.456—holotype of *annamensis*), Lang Bian Peak (BM 1946.1.5.27–30—syntypes of *uniformis*), southern Annam (CAS 73736). Cochin-China (MHNP 08–51, 98–20). Cambodia (NHMW 16183).

MALAYA: Pulo Jarak (NMS 9933); Penang Island (BM 96.6.35.46, 98.9.22.42). Perak: Larut Hills (BM 1900.6.14.24), Wellesley (BM 96.6.25.29). Pahang (NMS 2 unnumbered): Bukit Chintamani (NMS unnumbered). Selangor: Bukit Lagong (NMS unnumbered), Ban Sai Kam (BM 1903.4.13.74).

?Java (MHNP 3298—holotype, 3297–C2323—holotype of *quadrimaculata*).

?India (BM 116a).

Specimens examined.—85.

Calamaria septentrionalis Boulenger. Figure 59.

Calamaria septentrionalis Boulenger, 1890, Proc. Zool. Soc. London, **1890**, p. 34—Kiukiang and Hong Kong; 1894, Cat. Snakes Brit. Mus., **2**, p. 349, pl. 20, fig. 1; 1899, Proc. Zool. Soc. London, **1899**, p. 165; Wall, 1903, Proc. Zool. Soc. London, **1903**, p. 93; Mocquard, 1905, Bull. Soc. Philom. Paris, (9), **7**, p. 318; Stanley, 1914, Jour. N. China Branch Roy. Asiatic Soc., **45**, p. 26; Mell, 1922, Arch. Naturg. Berlin, **88**, p. 122; 1929, Lingnan Sci. Jour., **8**, p. 212; 1930, Sitz. Ges. Naturf. Freunde Berlin, **1930**, p. 323; Werner, 1924, Denks. Akad. Wiss. Wien, **99**, p. 48; 1929, Zool. Jahrb., (Syst.), **57**, p. 174; Parker, 1925, Ann. Mag. Nat. Hist., (9), **15**, p. 303; Stejneger, 1925, Proc. U. S. Nat. Mus., **66**, p. 91; Schmidt, 1927, Bull. Amer. Mus. Nat. Hist., **54**, p. 538; Pope, 1929, Bull. Amer. Mus. Nat. Hist., **58**, p. 454; 1935, Rept. China, p. 306, pl. 12, figs. K–P; Fan, 1931, Bull. Dept. Biol. Col. Sci. Sun Yat Sen Univ., no. 11, p. 106; Bourret, 1935, Bull. Gen. Instrut. Publ., no. 10, p. 8; *ibid.*, no. 11, p. 6; 1937, *ibid.*, no. 13, p. 33; *ibid.*, no. 15, p. 77; 1939, *ibid.*, no. 17, p. 23; *ibid.*, no. 18, p. 28; 1941, *ibid.*, no. 21, p. 14; 1944, *ibid.*, no. 25, p. 41; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 194; Romer, 1961, Mem. Hong Kong Nat. Hist. Soc., no. 5, p. 6.

Syntypes.—British Museum (Natural History) 91.1.28.1–2 (=1947.3.6.60–61).

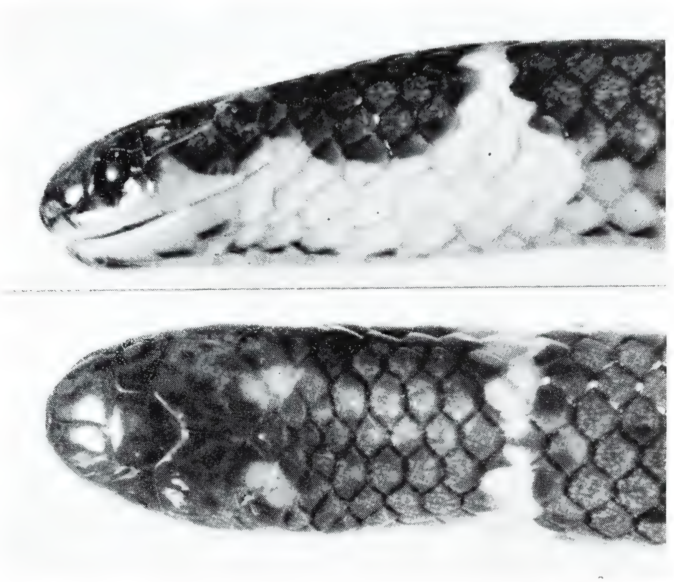

FIG. 59. *Calamaria septentrionalis* (CNHM 7140).

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; preocular present; mental not touching anterior chin shields; tail as thick as body, not tapered, end rounded.

Description.—Rostral broader than high, portion visible from above less than one-third length of prefrontal suture; prefrontal slightly shorter than length of frontal, touching first 2 supralabials; frontal $1\frac{3}{4}$ to $2\frac{1}{2}$ times width of supraocular; length of frontal about three-fourths that of parietal; parietal $1\frac{1}{3}$ to $1\frac{1}{2}$ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal slightly smaller than or equal to postocular; preocular usually higher than postocular, the two subequal in width; neither ocular as high as eye; eye usually larger than eye-mouth distance; 4 supralabials, second and third entering orbit, fourth largest, third one-half to three-fifths length of second, first and third subequal; mental triangular, separated from anterior chin shields by first infralabials; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting in midline; 3 gulars in midline between second chin shields and first ventral.

Body thickness index 0.021–0.047 (4 specimens); tail short, not tapering, tip broadly rounded; dorsal scales not reduced to 4 rows on tail (Fig. 10A).

Hemipenis forked opposite fourth subcaudal; retractor muscle beginning opposite seventh subcaudal (1 specimen).

Eight (8 specimens) to 9 (2) modified maxillary teeth.

Ventrals: males, 148–166 (mean 156.5; N=29); females, 168–188 (mean 175.6; N=29). Subcaudals: males, 15–19 (mean 16.5; N=28); females, 6–11 (mean 9.1; N=30).

Total length: males, 111–344 mm.; females, 117–384 mm. Ratio of tail to total length: males, 0.063–0.086 (mean 0.073; N=21); females, 0.026–0.043 (mean 0.035; N=31).

Color dark brown or black above; each dorsal scale with many small light dots forming a network; first and second scale rows yellowish with dark dorsal and ventral edges; the amount of dark pigment increasing rapidly in second row, second row similar to dorsal rows beyond the first fourth of body; a narrow yellow ring usually present about 6 to 8 scales behind head; head dark above; lower two-thirds of supralabials yellowish; underside of head yellowish with small dark spots; ventrals yellowish, immaculate except for dark spot at the extreme lateral corners; tail yellowish below with a broad median black stripe, the yellowish color often extending upward to form bars or spots on the lateral surface of the tail. In life the lower parts are coral red (Pope, 1935).

TABLE 55.—Variation in Samples of *Calamaria septentrionalis*.

		Ventrals		Subcaudals		Tail ratio[1]	
Regions	No.	Range	Mean	Range	Mean	Range	Mean
				MALES			
Tonkin	6	148–62	154.7	15–17	16.3	76–83	79
Fukien	2	155–60	157.5	17	17.0	65–81	73
Kwangsi	12	148–61	156.0	15–19	16.3	63–83	72
Hunan	2	154–55	154.5	16–17	16.5	76–86	81
Anhwei	3	152–61	157.7	16–18	17.3	65–82	74
Chekiang	2	155–59	157.0	15–18	16.5	72–73	72
Hong Kong	1	166	..	17	..	78	..
				FEMALES			
Tonkin	2	168–71	169.5	9–10	9.5	31–28	35
Hainan	1	188	..	8	..	35	..
Fukien	3	172–78	175.7	8–9	8.3	28–38	33
Kwangsi	10	170–83	175.5	6–10	8.7	26–41	34
Hunan	1	171	..	9	..	36	..
Anhwei	7	170–84	178.7	8–11	10.0	32–36	33
Chekiang	5	169–75	172.0	7–10	8.8	34–43	38

[1] Ratio in thousandths of total length.

Individual variation.—These snakes are remarkably uniform. About one-fourth have the eye diameter equal to the eye-mouth distance. One specimen has a few small black spots scattered over the ventrals. Another has the third supralabial fused to the postocular on its left side.

Geographic variation.—This species does not even show the usual amount of local differentiation in ventral and subcaudal counts (Table 55).

Distribution.—From northern Indo-China through eastern China as far north as Chekiang Province (Fig. 74).

CHINA: Kiukiang Mountains (BM 91.1.28.1-2—syntypes). Chekiang: Hangchow (MCZ 16187[2]), Mukan Shan (USNM 64016-18), Nengpo (NMB 7481), Chu Shan Islands (BM 92.12.12.5), mainland opposite Chu Shan Islands (BM 93.4.20.26). Anhwei: Wuhu (AMNH 24535, 23533-35; BM 1933.11.12.2), Ningkwo (AMNH 24618-19, 25572; CNHM 7141). Southwestern Hunnan (USNM 63191-93). Kwangsi (ZSBS 169/47): Pingsiang (MCZ 25895; NHMW 16185[5]; NMB 5865; SNG 19437-38; UMMZ 67195), Nanan (AMNH 31770-78), Nangaodsu Mountain (NHMW 16184), Loshing (MCZ 32419-20). Northern Hainan (NMHW 16186). Fukien: Foochow (USNM 65414), Chungan (AMNH 34635), Nanping (AMNH 33411), Kuatun (BM 99.4.24.37).

HONG KONG (CNHM 142361).

INDO-CHINA. Tonkin: Laokay (MHNP 02-78, 08-190), Gao Bang (BM 96.4.21.1; MHNP 96-27, 04-390), Ngan Son (MHNP 34-418, 58457), Thai Nguyen (BM 1924.12.9.197).

No data (MHNP 35-316).

Specimens examined.—60.

Calamaria lowi Boulenger

The only consistent difference between *Calamaria gimletti* (Malaya) and *lowi* (Borneo) is that in the former the mental shield is separated from the chin shields by the first infralabials, but touches the chin shields in Bornean *lowi* (Table 56). They also differ in subcaudal counts (Table 57). Otherwise these forms are very similar, having reduced orbital regions, high ventral counts (Table 57), and yellow spotting on the body and tail. Though the Malayan form is clearly conspecific with the Bornean one, we are designating it a sub-

TABLE 56.—Frequency Distribution of Forms of *Calamaria lowi* with Respect to Certain Characters.

Form	Region	Supralabials in orbit		Infralabials		Mental touching chin shields	
		1	*2*	*4*	*5*	Yes	No
l. gimletti	Malaya	0	13	2	11	0	13
l. gimletti	Riouw Arch.	0	2	0	2	0	2
l. lowi	Borneo	44	13	21	46	57	0
l. wermuthi	Java	0	1	1	0	1	0

species, *C. lowi gimletti* Boulenger, because of the differences shown in Tables 56 and 57.

A single specimen from Java (ZMB 29690) is similar to *lowi lowi* (Borneo) but differs in having a much smaller eye, the frontal wider than the parietal, and cream-colored ventrals throughout the entire length of the body. This Javan specimen differs from the Malayan form of *lowi* even more (Table 56) and we are designating it the holotype of a distinct subspecies, *C. lowi wermuthi.*

The differences among these forms are not as great as the differences between good sympatric species.

Diagnosis.—Maxillary teeth modified; second and third or only third supralabial entering orbit; no preocular; posterior chin shields meeting in midline; supraocular distinct from postocular.

TABLE 57.—Geographic Variation in Ventral and Subcaudal Counts of *Calamaria lowi.*

Form	Region	No.	Ventrals		Subcaudals	
			Range	Mean	Range	Mean
				MALES		
l. gimletti	Malaya	6	161–202	188.8	14–18	17.2
l. gimletti	Riouw Arch.	2	163–184	173.5	20	. .
l. lowi	Borneo	21	190–222	203.2	17–26	21.8
				FEMALES		
l. gimletti	Malaya	6	215–249	230.8	10–12	11.2
l. lowi	Borneo	33	218–254	230.5	11–18	15.7
l. wermuthi	Java	1	256	. .	11	. .

Calamaria lowi lowi Boulenger. Figure 60.

Calamaria lovii Boulenger, 1887, Ann. Mag. Nat. Hist., (5), **19**, p. 169, fig.—Rejang River, Sarawak; 1894, Cat. Snakes Brit. Mus., **2**, p. 350, pl. 30, fig. 2; Bartlett, 1895, Sarawak Note Book, no. **1**, p. 85.

Calamaria lowi, Mocquard, 1890, Nouv. Arch. Mus. Paris, (3), **2**, p. 120; Boettger, 1898, Kat. Rept. Samm. Senck. Naturf. Ges., pt. 2, p. 85; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 177; Dunn, 1923, Jour. Malayan Branch Roy. Asiatic Soc., **1**, p. 2; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 174; de Haas, 1950, Treubia, **20**, p. 570; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 199.

Calamaria ventralis Cochran, 1923, Proc. Biol. Soc. Washington, **36**, p. 91—Sungai Merah, southeastern Borneo; Werner, *loc. cit.*, p. 174; de Haas, *loc. cit.*, p. 575; Marx and Inger, *loc. cit.*, p. 206.

Calamaria javanica lineata Brongersma, 1928, Zool. Anz., **75**, p. 256—Long Petah, eastern Borneo; Werner, *loc. cit.*, p. 174; de Haas, *loc. cit.*, p. 568; Marx and Inger, *loc. cit.*, p. 202.

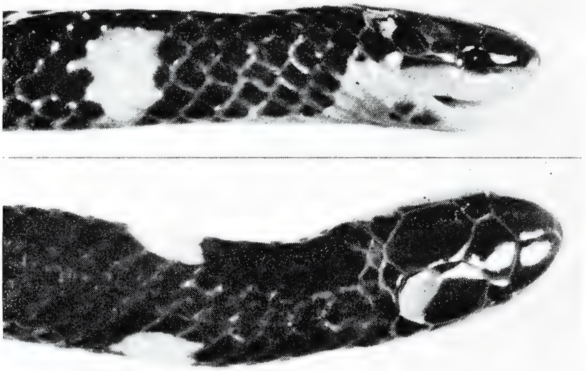

FIG. 60. *Calamaria lowi lowi* (CNHM 131606).

Holotype.—British Museum (Natural History) 87.2.7.18.

Taxonomic notes.—*Calamaria ventralis* was originally distinguished from *lowi* on the basis of the number of supralabials touching the eye; the second and third bordered the eye in the holotype of *ventralis* whereas only the third was thought to do so in *lowi*. The holotype of *C. javanica lineata* does not differ from *ventralis* except in those characters, such as ventrals and subcaudals, that show sexual dimorphism. These two specimens and a third from Indonesian Borneo (NMB 14335) agree in the relationship between supralabials and eye.

Most of the known specimens of *lowi* have only the third labial bordering the eye. However, one population only 150–200 kilometers from the type locality has two labials bordering the eye. In another sample of 21 from Niah, Sarawak, one snake has two labials entering the eye on the right side and only one on the left. Three other specimens from separate localities in Sarawak and North Borneo have two labials bordering the eye.

Thus the states of this character seem to be scattered in Borneo and do not form the consistent pattern one would expect of subspecies. Furthermore, variation in this character is not correlated with that of any other character. We are obliged to treat *C. ventralis* Cochran and *C. javanica lineata* Brongersma as strict synonyms of *lowi*.

Diagnosis.—Mental touching chin shields; ventrals brown or yellow marked with dark pigment.

Description.—Rostral slightly higher than wide, portion visible from above one-half to two-thirds length of prefrontal suture; prefrontals longer than frontal, in contact with first two or three supralabials; frontal 2½ to 4⅓ times width of supraocular, about three-fourths length of parietals; parietal longer than prefrontal; paraparietal surrounded by 6 shields and scales; nasal moderately large, equal to or slightly smaller than postocular; no preocular; postocular not as deep as eye; eye small, about one-half eye-mouth distance; 4 supralabials, only third or second and third entering orbit, fourth longest, second longer than third, first smallest; mental triangular, touching first pair of chin shields; 4 or 5 infralabials, first 2 (if 4 infralabials) or 3 pairs touching anterior chin shields, both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Body thickness index 0.008–0.014 (8 specimens); tail short, thick, tapering slightly at end, no spine; dorsal scales reduce to 4 rows on tail opposite second to tenth subcaudal anterior to terminal scute.

Hemipenis forked opposite fourth to seventh subcaudal; retractor muscle beginning opposite tenth or eleventh subcaudal; calyces papillate (3 specimens).

Eight to 10 modified maxillary teeth (8 specimens).

Ventrals: males, 190–222 (mean 203.2; N=21); females, 218–254 (mean 230.5; N=33). Subcaudals: males, 17–26 (mean 21.8; N=21); females, 11–18 (mean 15.7; N=33).

Total length: males, 116–276 mm.; females, 142–316 mm. Ratio of tail to total length: males, 0.065–0.102 (mean 0.077; N=20); females, 0.031–0.052 (mean 0.043; N=33).

Color above dark brown usually with yellow spots on body; narrow light stripes, if present, formed by light scales, a complete or narrowly interrupted yellow ring around body at vent; usually a small yellow spot at tip of tail; head dark brown above with obscure lighter markings; dark pigment extending on to upper third of last three supralabials; remainder of supralabials, nasal, adjacent corner of prefrontal, and rostral yellowish; underside of head yellow, usually with brown speckling; yellow of side of head extending dorsally on to neck; ventrals cream in anterior portion of body, becoming increasingly darker and almost uniformly dark brown in posterior part of body; the invasion of dark pigment begins at lateral and anterior edges of ventrals; one specimen with broad yellow bars crossing belly and five with yellow ventrals having large, irregular brown squares; subcaudals dark brown, uniform or with light streak or spots in each row.

Individual variation.—One snake (CNHM 131614) has a small preocular on each side, excluding the prefrontal from the eye.

One specimen (CNHM 131619) has no eye on the right side; the supraocular and postocular are fused on that side. A second specimen (SM Cd.5.26.20) has the supraocular fused with the postocular on both sides; but the eyes are present.

Distribution.—Borneo (Fig. 61).

SARAWAK. First Division: Kuching (BM 1933.6.20–22), Sadong (SM Cd.5.26.20d), Gunong Temiang (SM 352). Third Division: Mount Dulit (BM 1933.20.23–25), Rejang River (BM 87.2.7.18—holotype), Nanga Tekalit (CNHM 136336). Fourth Division: Niah River (BM 92.10.7.9), Niah (CNHM 109974–75, 129001–03, 131605–19), Baram River basin (BM 97.3.4.8–9, 1902.11.25.19; NHMW unnumbered; SNG 19439), Long Mujan (CNHM 72373; MCZ 16364–67; NMS 55, 1 unnumbered; SU 8525), Sungei Seran, Labang (CNHM 148355–58). Fifth Division: Trusan River (SM Cd.5.26.20b–c).

NORTH BORNEO: Jesselton (CNHM 109976); western North Borneo (SM Cd.5.26.f).

INDONESIAN BORNEO: Balikpapan (NMB 14335), Long Petah (ZMA unnumbered-holotype of *javanica lineata*), Sungai Merah (USNM 57637—holotype of *ventralis*).

No data (BM 97.3.8–9, 1 unnumbered).

Specimens examined.—57.

Calamaria lowi wermuthi new subspecies

Holotype.—Zoologisches Museum Berlin 29690, a female from Java collected by Robert Mertens.

Diagnosis.—Second and third supralabials entering orbit; menta touching anterior chin shields; ventrals uniformly cream colored except at their lateral extremities.

Description of holotype.—Rostral higher than wide, portion visible from above two-thirds length of prefrontal suture; prefrontal longer than frontal, touching first two supralabials; frontal 3¾ width of supraocular, about ¾ length of parietal; parietal longer than prefrontal; nasal slightly smaller than postocular; no preocular; postocular as deep as eye; eye small, less than half eye-mouth distance; 4 supralabials, second and third touching eye, second and fourth subequal and about 2½ times length of third, which is smallest; mental triangular, touching first pair of chin shields; 4 infralabials, first 2 pairs touching anterior pair of chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Tail short, thick, tapering abruptly at end; dorsal scales reduce to 4 rows on tail opposite fourth subcaudal anterior to terminal scute.

Ventrals 256; subcaudals 11; total length 315 mm.; ratio of tail length to total length 0.025.

Body dark brown above; anteriorly first 3½ scale rows immaculate cream-colored; posteriorly dark dorsal color covers all of fourth row, upper half of third row, adjacent edges of first and second rows, and adjacent edges of first row and ventrals; posteriorly scales of fifth, sixth, and seventh rows with small light dots in their centers; a vertebral row of nineteen squarish yellow spots from head to base of tail, each spot occupying parts of two to four adjacent scales and successive spots separated by six to twelve scales; a cream-colored ring around body at vent; a cream-colored spot dorsally at tip of tail; head dark brown above with obscure lighter markings, dark pigment ending on upper edge of fourth supralabial; supralabials, lower half of rostral, and entire underside of head cream-colored; cream color extends posteriorly in a horizontal band, not extending upward onto parietals or neck; all ventrals cream-colored, the posterior ones with dark brown lateral edges; underside of tail brownish with a yellowish streak down the center of each row of subcaudals.

Distribution.—Java (Fig. 61).

Calamaria lowi gimletti Boulenger

Calamaria gimletti Boulenger, 1905, Ann. Mag. Nat. Hist., (6), **15**, p. 456—Kelantan, Malaya; 1912, Vert. Fauna Malay Penin., Rept., p. 220; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 174; Smith, 1930, Bull. Raffles Mus., no. 3, p. 59; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 201.

Calamaria doerianense Brongersma, 1928, Zool. Anz., **75**, p. 255, 2 figs.—Pulau Durian, Riouw Archipelago; Werner, *loc. cit.*, p. 174; de Haas, 1950, Treubia, **20**, p. 566; Marx and Inger, *loc. cit.*, p. 201.

Calamaria pavimentata (non Duméril and Bibron), Sclater, 1891, Snakes Indian Mus., p. 10.

Calamaria javanica (non Boulenger), Wall, 1921, Rec. Indian Mus., **22**, p. 729; Smith, 1930, *loc. cit.*, p. 59.

Calamaria melanota (non Jan), Chasen and Smedley, 1927, Jour. Malayan Branch Roy. Asiatic Soc., **5**, p. 353; de Haas, *loc. cit.*, p. 571 (part).

Calamaria fraseri Taylor, 1962, Univ. Kansas Sci. Bull., **31**, p. 254, fig. 15—Fraser's Hill, Malaya, 3800 feet.

Holotype.—British Museum (Natural History) 1905.2.7.7.

Taxonomic notes.—The holotype of *doerianense* cannot be distinguished from *gimletti*. The second specimen from the Riouw Archipelago is also indistinguishable from Malayan *gimletti* and supports our decision to synonymize *doerianense*.

Wall (1921) stated that the Indian Museum specimen (no. 4450) does not have a postocular and that the subcaudals are entire. This snake, which we have examined, has a distinct postocular and paired subcaudals and is a typical *gimletti*.

Two snakes from Fraser's Hill, Malaya differ from all other Malayan specimens of *gimletti* in having much lower ventral counts (males 161, 164 as compared to 184–202). As the specimens from Fraser's Hill cannot otherwise be distinguished from the Malayan snakes we have seen, we refer *C. fraseri* Taylor (type locality Fraser's Hill) to the synonymy of *C. l. gimletti*.

Diagnosis.—Mental not touching anterior chin shields.

Description.—Rostral wider than high or higher than wide, portion visible from above about half length of prefrontal suture; prefrontal as long as frontal, touching first 2 supralabials; frontal 2½ to 4 times width of supraocular, length about two-thirds that of the parietal; parietal 1⅓ to 1½ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal equal to or smaller than postocular; no preocular; postocular not as deep as eye; eye less than eye-mouth distance; 4 supralabials, second and third entering orbit, fourth longest, third half of second, first slightly longer than third; mental triangular, not touching chin shields; usually 5 infralabials, 3 touching anterior chin shield; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Tail short, not tapering, tip blunt; dorsal scales reduce to 4 rows on tail opposite first to fifth subcaudal anterior to terminal scute except for one specimen with five scale rows anterior to terminal scute.

Eight to 9 modified maxillary teeth (5 specimens).

Ventrals: males, 161–202 (mean 182.3; N=9); females, 215–249 (mean 230.8; N=6). Subcaudals: males, 14–20 (mean 17.2 N=9); females, 10–12 (mean 11.2; N=6).

Total length: males, 149–192 mm.; females, 161–269 mm. Ratio of tail to total length: males, 0.062–0.084 (0.068; N=7); females, 0.030–0.037 (mean 0.035; N=6).

Color dark brown above; lower halves of supralabials yellow; with or without narrow yellow rings or small spots dorsally; ventrals and subcaudals uniformly yellowish except at extreme lateral corners.

Geographic variation.—Despite the wide range of variation in ventral counts, the specimens from Negri Sembilan (the only locality from which we have a series) show the typical restriction of individual variation locally. The three males from that locality have 195–202 ventrals; the three females have 215–229. The difference between these and snakes from other areas is evidence of local differentiation.

Distribution.—The Malay Peninsula, Riouw Archipelago, and Aor Island (Fig. 61).

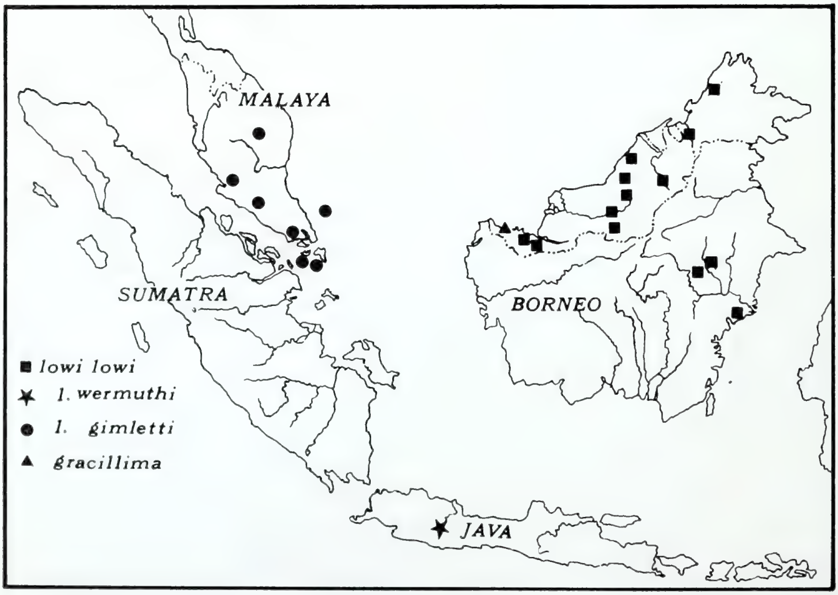

Fig. 61. Distributions of *Calamaria gracillima* and *C. lowi*. No precise locality in Java.

MALAYA. Johore (ZSI 4450): Gunong Pulai (NMS unnumbered). Pahang: Fraser's Hill (EHT-HMS M29, holotype of *fraseri;* NMS unnumbered). Selangor: Bukit Lagong Forest Reserve (NMS 18101). Negri Sembilan: Tampin (BM 1931.5.14.3–8). Kelantan (BM 1905.2.7.7—holotype).

AOR ISLAND (NMS unnumbered).

RIOUW ARCHIPELAGO. Durian Island (ZMA unnumbered—holotype of *doerianense*). Gallang Island (NMS unnumbered).

Specimens examined.—14.

Calamaria gracillima (Günther)

Typhlocalamus gracillima Günther, 1872, Proc. Zool. Soc. London, **1872**, p. 594, pl. 39, fig. A—Sarawak.

Calamaria gracillima, Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 350; Bartlett, 1895, Sarawak Note Book, no. 1, p. 85; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 178; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 174; de Haas, 1950, Treubia, **20**, p. 567; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 202.

Holotype.—British Museum (Natural History) 72.2.19.77.

Taxonomic notes.—The fusion of the supraocular and postocular, one of the striking characteristics of *gracillima,* appears rarely in *C. lowi.* These two species differ consistently, however, in other characters: ventral counts (more than 290 in *gracillima,* less than 250 in *lowi*), relative widths of frontal (more than 5 times width of supraocular in *gracillima,* less than 5 in *lowi*), and relative lengths of tails.

Calamaria gracillima and *lowi* are apparently sympatric. The only definite locality for *gracillima* (other than "Borneo" or "Sarawak") is Matang; *lowi* has been collected at Kuching, 30 miles away. From personal field experience in that part of Sarawak, we judge that a species found at Kuching can live as well at Matang (and vice versa). Both areas were originally covered with lowland rain forest. Although Matang rises 300 to 500 meters above sea level, its forest does not differ in character from that of any low hill in that corner of Sarawak.

Diagnosis.—Maxillary teeth modified; second and third supralabials entering orbit; no preocular; supraocular fused with postocular.

Description.—Rostral higher than wide, portion visible from above less than half length of prefrontal suture; prefrontal much longer than frontal, touching first 2 supralabials; frontal quadrangular, 6 to 8 times width of supraocular, length about two-thirds length of parietal; parietal 1¼ length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than eye; no preocular; postocular fused with supraocular; eye very small, less than half eye-mouth distance; 4 supralabials, second and third entering orbit, second and fourth equal, third one-half of second, first slightly larger than third; mental triangular, not touching chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Tail short, not tapered, tip blunt; dorsal scale rows reduce to 4 rows on tail opposite fifth to seventh subcaudal anterior to terminal scute.

Ten modified maxillary teeth (1 specimen).

Ventrals: male, 295; females, 290–304 (N=2). Subcaudals: male, 15; females, 12–13 (N=2).

Total length: male, 285 mm.; females, 285–287 mm. Ratio of tail to total length: male, 0.035; females, 0.028–0.035 (N=2).

The ventral count of the holotype is given incorrectly in the original description as 320; the correct count is 290.

Color dark brown above; a series of widely spaced, vertical yellow spots on the sides in anterior third of body; a similar yellow spot at root of tail and one or two a short distance anterior to vent; dark brown below, each ventral and subcaudal lighter in its posterior half.

Distribution.—Western Borneo (Fig. 61).

SARAWAK (BM 72.2.19.77—holotype). First Division: Matang (BM 73.4.25.6).

BORNEO (ZMB 7650).

Calamaria rebentischi Bleeker

Calamaria rebentischi Bleeker, 1860, Nat. Tijds. Ned. Indië, **21**, p. 293—Singkawang, Borneo; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 343, pl. 18, fig. 3; Bartlett, 1895, Sarawak Note Book, no. 1, p. 84; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 169; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 172; de Haas, 1950, Treubia, **20**, p. 573; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 205.

Holotype.—British Museum (Natural History) 63.12.4.27 (1946.1.4.68).

Taxonomic notes.—This species is very similar to *ceramensis* de Rooij from which it differs in the shape of tail and coloration (de

Rooij, 1917). In *ceramensis* the tail in both sexes is tapered gradually throughout its length and ends in a sharp point; in *rebentischi* the tail tapers only in the distal fifth to a blunt tip. *C. ceramensis* has a light nuchal collar which is lacking in *rebentischi*.

The differences between these two species are slight and were it not for their wide geographic separation we might have considered them conspecific. There is no reason for doubting the locality given by Bleeker for *rebentischi*.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; no preocular; mental not touching anterior chin shields; tail tapering in posterior fifth; dorsal scales yellow with a dark brown network; no stripes above first scale row; no nuchal collar.

Description.—Rostral wider than high, portion visible from above equal to two-thirds length of prefrontal suture; prefrontal shorter than frontal; frontal hexagonal, 2⅔ width of supraocular, shorter than parietal; parietal longer than prefrontal; paraparietal surrounded by 5 shields and scales; no preocular; postocular not as high as eye; eye smaller than eye-mouth distance; 5 supralabials, third and fourth entering orbit; mental separated from anterior chin shields by first infralabials; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting in midline.

Tail tapering in posterior fifth; dorsal scales reduce to 4 rows at the terminal scute.

Seven modified maxillary teeth.

Ventrals 140 in male; subcaudals 29. Total length 270 mm.; ratio of tail length to total length 0.152.

Color dark brown above, yellowish below; dorsal scales yellowish-brown, each with a dark network and dark edges; scales of first row with yellow centers and dark edges; head dark brown above and on sides including all of the first three supralabials and upper half of the fifth supralabial; rest of upper lip and underside of head yellow with brown spots on labials and chin shields; ventrals and subcaudals yellow with brown lateral tips; a few small brown spots mid-ventrally on tail.

Distribution.—Western Borneo (Fig. 58).

INDONESIAN BORNEO: Singkawang (BM 63.12.4.27—holotype).

Calamaria ceramensis de Rooij

Calamaria ceramensis de Rooij, 1913, Bijdr. Dierk., **19**, p. 26—Honitétu, Ceram; 1917, Rept. Indo-Austr. Arch., **2**, p. 169; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173; de Haas, 1950, Treubia, **20**, p. 565; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 200.

Calamaria jeudei Kopstein, 1926, Zool. Meded., **9**, p. 108—Saparua Island, Molucca Islands; Werner, *loc. cit.*, p. 173; de Haas, *loc. cit.*, p. 569; Marx and Inger, *loc. cit.*, p. 202.

Syntypes.—Zoologisch Museum Amsterdam 10083[2].

Taxonomic notes.—Kopstein (1926) states that *jeudei* differs from *ceramensis* in ventral and subcaudal counts and in the width of the frontal. Although he gave the ventral count of the holotype of *jeudei* as 177, the correct count is 146. This specimen is a male and the difference between its count and those of the female syntypes of *ceramensis* represents normal sexual dimorphism. Additional specimens of both sexes of *ceramensis* support this conclusion and bridge the gap in the width of the frontal. Saparua Island, the type locality of *jeudei*, is less than ten kilometers south of Ceram.

For comparison with the very similar species *rebentischi* see above.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; no preocular; mental not touching anterior chin shields; tail tapering from its base to a point; light nuchal collar present.

Description.—Rostral wider than high, portion visible from above ½ to ⅔ length of prefrontal suture; prefrontal shorter than frontal, touching first 3 supralabials; frontal hexagonal, 2 to 3½ times width of supraocular, about four-fifths length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 5 shields and scales; nasal slightly smaller than postocular; no preocular; postocular not as high as eye; eye equal to or smaller than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth largest, second slightly larger than first, third and fourth subequal to first; mental triangular, not touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting in midline; 3 gulars in midline between second pair of chin shields and first ventral.

Body thickness index 0.026–0.037 (2 specimens); tail moderately long, tapering gradually to point; dorsal scales reduce to 4 rows opposite second to eighth subcaudal anterior to terminal scute.

Cloaca of female cardioid (1 specimen).

Seven to 9 modified maxillary teeth (5 specimens).

Ventrals: males, 139–146 (mean 142.3; N=3); females, 148–165 (mean 156.1; N=7). Subcaudals: males 28–30 (mean 28.6; N=3); females, 17–21 (mean 19.3; N=7).

Total length: males, 152–267 mm.; females, 209–309 mm. Ratio of tail to total length: males, 0.125–0.150 (mean 0.135; N=3); females, 0.071–0.087 (mean 0.081; N=7).

Color dark brown above, yellow below; dorsal scales yellowish-brown with a dark network or dark brown with a light network; dark spots about half a scale in area, scattered over most of body; usually centers of scales in first row yellow; narrow, light, nuchal ring crossing rear of parietals, width of ring equal to that of one dorsal scale, bordered posteriorly by a ring of dark scales; head dark brown above, the dark pigment covering upper halves of supralabials, occasionally covering all of first two supralabials; rest of supralabials and underside of head yellowish with small brown spots on infralabials and anterior chin shields; ventrals yellow with dark lateral tips, about one-third of specimens with small dark dots across anterior edges of ventrals; tail yellowish below, a dark median streak present or absent.

Individual variation.—A single specimen (ZSBS 947/20) has the second, third, and fourth supralabials entering the orbit on both sides; the prefrontal touches the first two supralabials only.

A second specimen (BM 1920.8.9.8) has the second to fourth supralabials entering the orbit on one side only.

Distribution.—Southern Moluccas.

CERAM: Honitetoe (ZMA 10083[2]—syntypes), Mansuela, 915 meters (BM 1920.8.9.8–9; ZSBS 947/20), Elpaputih Bay (RMNH 490); east Ceram (CNHM 83464; ZMA 10084).

SAPARUA (RMNH 5103—holotype of *jeudei*).

AMBON: Waai (CNHM 142242).

Specimens examined.—10.

Calamaria mecheli Schenkel. Figure 62.

Calamaria mecheli Schenkel, 1901, Verh. Ges. Basel, **13**, p. 165, fig. 4—Indragiri, Sumatra; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 169; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 173; de Haas, 1950, Treubia, **20**, p. 571; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 204.

Holotype.—Naturhistorisches Museum Basel 1699.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; no preocular; mental separated from anterior chin shields; a continuous dark vertebral stripe; tail tapering to a point.

Description.—Rostral wider than high; portion visible from above one-half length of prefrontal suture; prefrontal slightly shorter than frontal, touching first 3 supralabials; frontal hexagonal, 2⅓ to 3½ times width of supraoculars, about three-fourths length of parietal; parietal 1½ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; no preocular; postocular not as high as eye; eye equal to or slightly less than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth the largest and more than combined length of third and fourth, second larger than first, third and fourth subequal and smallest; mental triangular, usually separated from anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; both pairs of chin shields meeting in midline; 3 gulars in midline between posterior chin shields and first ventral.

Tail tapering slightly from base, more sharply near end to a point; dorsal scales reduce to 4 rows on tail opposite second or third subcaudal from terminal scute or six rows of dorsals to terminal scute.

Eight to 9 modified maxillary teeth (3 specimens).

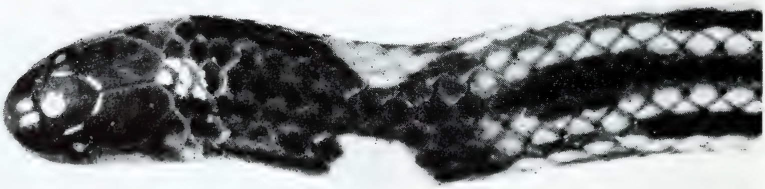

FIG. 62. *Calamaria mecheli* (NHMW 17025).

Ventrals: male, 174; females, 167–195 (mean 187.7; N=6). Subcaudals: male, 28; females, 12–16 (mean 13.8; N=6).

Total length: male, 249 mm.; females, 204–247 mm. Ratio of tail to total length: male, 0.116; females, 0.046–0.053 (mean 0.049; N=5).

Body brown above, cream colored below; dorsal scales light brown with a fine dark network; a narrow dark stripe along adjacent edges of ventrals and first scale row; scales of first row with light centers forming a light longitudinal stripe; a dark stripe occupying second scale row and usually part of first; a dark stripe formed by black centers of vertebral scales; a dark longitudinal stripe sometimes present on fifth or on fourth and fifth scale rows; some specimens with a pair of light paravertebral spots above base of tail and another pair near tip; head purplish brown above with obscure darker markings; dark pigment covering upper third or more of supralabials with narrow streaks along sutures; rest of supralabials and underside of head cream colored, several dark spots on mental and anterior infralabials; ventrals cream colored except at lateral edges; subcaudals cream colored with or without a narrow dark midventral stripe.

Individual variation.—The specimen from Deli is the only one with the mental touching the anterior chin shields. It also has the lowest female ventral count (167, the next higher is 186). These differences may represent geographic variation, but with the small sample known the type of variation involved cannot be verified. Geographic variation in the relationship of the mental and chin shields is known in other species of the genus (e.g., *lowi*).

Distribution.—Sumatra (Fig. 58).

SUMATRA (RMNH 10467). Sumatera Utara: Deli (UZMO unnumbered). Sumatera Tengah: Ajer Mantjoer (MCG 6774), Padang (NHMW 17025). Sumatera Selatan: Indragiri (NMB 1699—holotype, 1700–01—paratypes).

Specimens examined.—7.

Calamaria alidae Boulenger. Figure 63.

Calamaria alidae Boulenger, 1920, Ann. Mag. Nat. Hist., (9), **5**, p. 282—Lebong Tandai, Benkulen, Sumatra; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171; de Haas, 1950, Treubia, **20**, p. 564; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 200.

Holotype.—British Museum (Natural History) 20.1.16.22 (1946.1.3.64).

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; no preocular; tail thick, not tapered, broadly rounded at end (Fig. 14A).

Description.—Rostral wider than high, portion visible from above one-half length of prefrontal suture; prefrontal equal in length to frontal, touching first 3 supralabials; frontal hexagonal, 2½ to 3 times width of supraocular, three-fourths length of parietal; parietal

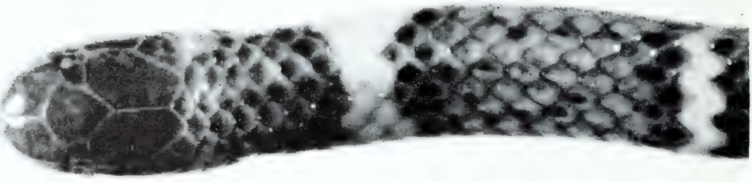

FIG. 63. *Calamaria alidae* (NHMW 16996).

about 1½ times length of prefrontal; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; no preocular; postocular subequal to eye; eye smaller than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth longest, as long as third and fourth combined, first 4 supralabials subequal or first and second larger; mental triangular, touching or separated from anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting in midline; 3 gulars in midline between second chin shields and first ventral.

Body thickness index 0.012 (1 specimen); tail thick, not tapered, ending bluntly (Fig. 14A); dorsal scales reduce to 4 rows on tail opposite third to fourth subcaudal anterior to terminal scute.

Nine or 10 modified maxillary teeth (3 specimens).

Ventrals: males, 185–203 (mean 193.3; N=3); female, 231. Subcaudals: males, 22–27 (mean 24.0; N=3); female, 17.

Total length: males, 219–254 mm.; female, 289 mm. Ratio of tail to total length: males, 0.087–0.096 (mean 0.090; N=3); female, 0.048.

Body olive or dark brown with variable markings (see below); most of light dorsal scales with dark network; head brown above and on sides, the dark pigment covering the upper halves of the supralabials or reaching the lip on the anterior ones; rest of supralabials and underside of head yellow, with or without dusky markings on infralabials and anterior chin shields; ventrals yellow, dark brown spots at lateral tips, the brown area expanding in posterior portion of body to cover lateral quarters; small dark brown spots present or absent across anterior edges of ventrals; underside of tail yellow with median and lateral dark brown stripes.

Individual variation.—Two specimens have a dorsal pattern of light longitudinal stripes: a yellow stripe on first scale row, a second on second row, a third on fourth and fifth rows, and a fourth occupying vertebral row and adjacent edges of paravertebral rows. The width and position of these stripes shift slightly in the posterior part of the body.

One Padang animal has a narrow dark stripe occupying the centers of the vertebral scales and instead of alternating light and dark stripes, has a pattern of short dark dashes or interrupted lines on a light brown background.

A second Padang specimen is brown above with 18 yellowish transverse bars on the body, each bar one or two scales wide and crossing 7 or 8 scale rows medially; anteriorly these transverse bars are separated by 5 to 8 scales whereas posteriorly they are separated by 12 to 15 scales. The tail has two light transverse bars, the first forming a complete ring at the anus, the second restricted to the medial scale rows. The tip of the tail is white.

Distribution.—Western Sumatra (Fig. 58).

SUMATRA. Sumatera Tengah: Padang (NHMW 16373, 16996), Kaba Wetan (USNM 70955). Sumatera Selatan: Lebong Tandai (BM 20.1.16.22—holotype).

Specimens examined.—4.

Calamaria apraeocularis Smith

Calamaria apraeocularis Smith, 1927, Proc. Zool. Soc. London, **1927**, p. 224—Djikoro, Mount Bonthain, Celebes; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171; de Haas, 1950, Treubia, **20**, p. 564; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 200.

Holotype.—British Museum (Natural History) 1926.8.20.157.

Diagnosis.—Maxillary teeth modified; third and fourth supralabials entering orbit; no preocular; mental touching anterior chin shields.

Description.—Rostral wider than high, portion visible from above about one-third length of prefrontal suture; prefrontal shorter than frontal, touching first 3 supralabials; frontal hexagonal, 2⅔ to 3 times width of supraocular, about three-fourths length of parietal; parietals about 1½ times length of prefrontals; paraparietal surrounded by 6 shields and scales; nasal smaller than postocular; postocular not as high as eye; eye diameter less than eye-mouth distance; 5 supralabials, third and fourth entering orbit, fifth largest, second slightly larger than first and slightly narrower than combined lengths of third and fourth which are the smallest; mental triangular, touching anterior chin shields; 5 infralabials, first 3 touching anterior chin shields; second pair of chin shields meeting in midline; 4 gulars in midline between second chin shields and first ventral.

Body thickness index 0.007–0.013 (2 specimens); tail thick, not tapered, bluntly rounded at end; dorsal scales reduce to 4 rows on tail opposite first to fifth subcaudal anterior to terminal scute.

Eight or 9 modified maxillary teeth (3 specimens).

Ventrals: males, 178–190 (N=2); females, 218–220 (N=2). Subcaudals: males, 18–19; females, 10.

Total length: males, 148–150 mm.; females, 237–283 mm. Ratio of tail to total length: males, 0.067–0.068; females, 0.030–0.035.

Color dark purplish brown above, lighter below; scales of first two or three rows with yellowish posterior halves; remainder of scales purplish brown with lighter reticulations; some of dorsal scales with a dark central spot forming narrow longitudinal dark lines in anterior portion of body; head dark brown above, with obscure darker markings, dark pigment covering upper half or two-thirds of supralabials; remainder of supralabials yellowish; underside of head yellowish with dark spots on labials and chin shields; ventrals and subcaudals dark brown in anterior halves, yellowish in posterior halves.

Individual variation.—As noted by Smith (1927, p. 225), one of the paratypes (MCZ 25300) has only four supralabials on the right side as a result of the fusion of the second and third.

Ecological notes.—Smith (*ibid.*) collected these animals under stones on an open hillside at 1,200 meters above sea level. He also stated that their diet consisted of "worms."

Distribution.—Southwestern Celebes.

CELEBES: Mount Bonthain, Djikoro (BM 1926.8.20.157—holotype, 1926.8.20.158—paratype; MCZ 25265, 25300—paratypes).

Specimens examined.—4.

DOUBTFUL FORMS

Calamaria yunnanensis Chernov

Calamaria yunnanensis Chernov, 1962, Zool. Instit. Acad. U.S.S.R., Trudy, **30**, p. 383, fig., Tsindun [Ching-tung district], Yunnan Province, China.

The holotype of *C. yunnanensis* is in the Zoological Institute of the Academy of Sciences of the Chinese National Republic in Peiping and is not available for examination.

Chernov's (1962) original description of this snake rightly compared it to its probable relatives, *pavimentata* and *septentrionalis.* The male specimen has 4 supralabials, 173 ventrals, 20 subcaudals and a tail ratio of 0.082. Both *pavimentata* and *septentrionalis* have 4 supralabials. Males of *pavimentata* have 125–168 ventrals, 13–33 subcaudals, and tail ratios of 0.069–0.169. Males of *septentrionalis* have 148–162 ventrals, 15–19 subcaudals, and tail ratios of 0.063–0.086.

Chernov stated that the absence of light spots on the side of the tail and the presence of narrow, dark, elongated stripes along the body, dark edges on the ventrals, and a nuchal collar distinguished the Yunnan snake from the single *pavimentata* and two *septentrionalis* he examined. However, some of the *pavimentata* and *septentrionalis* we have seen resemble the Yunnan specimen in these characters (see Table 53, pp. 215 and 220).

Unfortunately, critical details, such as shape of the maxillary teeth, tail shape, and position of reduction to four dorsal scale rows on the tail, were omitted from the description.

The absence of a preocular is the only character that differentiates this snake from all specimens of *pavimentata* and *septentrionalis* examined. However, we have seen two species (*schlegeli* and *lumholtzi*) in which the preocular may be present or absent.

Given the information now available, a firm decision concerning this specimen cannot be made.

Calamaria pavimentata semidoliata Werner

Calamaria pavimentata var. *semidoliata* Werner, 1896, Verh. Zool. Bot. Ges. Wien, **47**, p. 18—Sumatra.

In the original description, Werner stated that a specimen he had received from G. Redemann of Antwerp had 23 narrow, black cross bars on the body, 139 ventrals, 27 subcaudals, and an entire anal; he gave no other details.

On the basis of this information, *semidoliata* differs from *pavimentata* (known only from the mainland) only in having narrow dark crossbands. But this statement assumes that Werner's specimen had 4 supralabials, the mental separated from the chin shields, and a preocular.

The color pattern described by Werner is exactly like that of *doderleini* (from Sumatra). However, *doderleini* has 5 supralabials and this does not satisfy the assumptions made in the preceding paragraph.

Without seeing Werner's specimen the status of this name cannot be determined. The present location of the specimen is unknown.

Calamaria occipitalis Jan

Calamaria occipitalis Jan, 1862, Arch. Zool. Anat. Phys., **2**, p. 9—Java; 1865, Icon. Ophid., **10**, pl. 3, fig. 1; Boulenger, 1894, Cat. Snakes Brit. Mus., **2**, p. 342; de Rooij, 1917, Rept. Indo-Austr. Arch., **2**, p. 162; Werner, 1929, Zool. Jahrb., (Syst.), **57**, p. 171; de Haas, 1950, Treubia, **20**, p. 572; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 204.

The original description and Jan and Sordelli's plate (1865) apply to a snake similar to *lumbricoidea, schlegeli cuvieri,* and *bicolor.* On the whole, *occipitalis* seems to be most similar to *lumbricoidae,* differing from that species in having the mental separated from the chin shields and a smaller eye than is usual in Javan *lumbricoidea.* It differs from *schlegeli cuvieri* in having a narrower frontal (about 1½ times supraocular width as compared to more than three times in *cuvieri*) and in having a preocular. It differs from *bicolor* in having a narrower frontal and a light parietal collar. The light parietal of *occipitalis* figured by Jan recalls a common pattern in Javan *lumbricoidea* and *cuvieri.*

Jan (1862) stated explicitly that his specimens had divided anal plates and this character is illustrated in the Iconographie (Jan and Sordelli, 1865). None of the more than twenty-six hundred specimens we examined had a divided anal shield. This character suggests that *occipitalis* may not be a species of *Calamaria* although the other characters illustrated are found in *Calamaria.*

NON-CALAMARIA

Maticora intestinalis (Laurenti)

Calamaria klossi Smith, 1926, Ann. Mag. Nat. Hist., (9), **18**, p. 79—Siberut Island; de Haas, 1950, Treubia, **20**, p. 569; Marx and Inger, 1955, Fieldiana, Zool., **37**, p. 203.

The holotype of *klossi* (BM 1926.3.18.18) has a fang at the front of the maxilla and distinct internasals and prefrontals. It differs in no character from typical *M. intestinalis.*

EVOLUTION AND SPECIATION

Phylogenetic relations of the genus Calamaria.—Despite its specialization, *Calamaria* has characters that are common to many genera of colubrids of all modes of life adopted by the family. Among these characters are longitudinal scale rows, paired subcaudals, conical mandibular and palatal teeth, and large bilaterally symmetrical shields on the head. Such characters are so widely distributed in the Colubridae that they tell us little of the phylogeny and evolution of *Calamaria.*

Other characters of *Calamaria* occur in enough burrowing snakes to suggest that convergence accounts for their distribution. Loss or fusion[1] among head shields, absence of keels and pits on the dorsal scales, absence of changes in scale row counts along the body, shortening of the tail, and reduction in the size of the head are typical of many burrowing colubrids. *Calamaria* in the Orient, *Aspidura* in Ceylon (Smith, 1943), *Calamelaps* in Africa (Loveridge, 1944), and *Stilosoma* in the United States (Highton, 1956) show all of these traits.

Adaptation to burrowing among colubrids takes two general forms. The first involves an enlarged rostral shield used as an augur. The rostral may be sharply pointed and curved upward as in *Heterodon,* or broadly flattened with free lateral edges as in *Phyllorhynchus* and *Lytorhynchus,* or curved downward with a sharp horizontal edge as in *Scaphiophis.* At least some of the snakes having these types of rostrals burrow by means of a twisting motion of the head; in *Heterodon* the head tends to rotate on the long axis (Davis, 1946). The internasals are often modified in this type of burrower, but the other head scales are not much affected. Body form is variable, some snakes being short and stout (e.g., *Heterodon*), some moderately stout and longer than one meter (e.g., *Scaphiophis*), and others small and slender (e.g., *Xenocalamus*). Scales may be smooth or keeled and usually the number of rows changes along the body. Charac-

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[1] Without detailed embryological studies, one cannot safely distinguish between loss or fusion in this case. For the sake of simplicity in language, we will use the word "loss" in this discussion to designate both possibilities.

TABLE 58.—Summary of Characters of Blunt-headed Burrowing Colubrids from Old World Tropics.

	Number of species	Loreal	Pre-ocular	Post-ocular	Tem-poral[1]	Inter-nasals	Anal single	Dorsal scale rows	Supra-labials	Maxil-lary teeth	Maxil-lary fangs	Poste-rior hypapo-physes
Indo-Malayan[2]												
Calamaria	50	0	0 or 1	1	0	0	+	13	4–5	6–12	0	0
Pseudorabdion	10	0 or +	1 or 0	1	0	2	+	15	5–6	8–21	0	0
Oxyrhabdium	2	+	0	1–2	1	2	+	15	6–8	25–36	0	+
Calamorhabdium	2	0	0	1	0	0	+	15	5	13	0	?
Rhabdophidium	1	0	1	1	0	2	+	15	5–6	10–12	0	0
Idiopholis	2	0	0	1	0	2(3)	+	15	6	20	0	0
Collorhabdium	1	0	1	1	0	2	+	15	5	?	0	?
India and Southeast Asia[3]												
Plagiopholis	4	0 or +	1	2	1	2	+	15	5–6	16–20	0	+
Aspidura	5	0	0 or 1	2	1	1	+	15–17	6	20–24	0	+
Blythia	1	0	0	1	1	2	0	13	5	20–22	0	+
Xylophis	2	+	0	1	1	2	+	13–15	5	28–30	0	+
Haplocercus	1	0	1	2	1	1	+	17	7	10–12	0	+
Africa												
Chilorhinophis	3	0	0 or 1	0 or 1	0	0	0	15	4	3–4	+	0
Calamelaps	2	0	0	0 or 1	0	2	0	19–21	5–7	4–5	+	0
Cynodontophis	1	0	1	1 or 2	1	2	0	15	7	2–3	+	0
Aparallactus	10	0	1	1 or 2	0	2	+	15	6–7	7–10	+	0
Elapocalamus	1	0	1	1	0	2	0	15	6	"few"	+	0
Miodon	8	0	1	1 or 2	1	2	0	15	7	3–4	+	0
Macrelaps	1	0	0	1	1	2	+	25–27	7	5	+	0
Polemon	1	0	1	2	1	2	+	15	7	4	+	0
Poecilopholis	1	0	1	2	1	0	0	15	5	10	0	0
Stenorhabdium	1	1	1	1	0	2	+	15	6	7	0	0

[1] Temporals here refer to scales separating supralabials from parietals.

[2] Peninsular Thailand, Malaya, East Indies, and Philippine Islands.

[3] Including Ceylon, but excluding peninsular Thailand. *Calamaria* has been omitted from this category as only 3 of its 50 species occur in this area.

teristically this "augur" or "shovel-snouted" type of burrowing colubrid lives in open, non-forested, and relatively dry country.

The second type of burrower, the one with which we are concerned, has a blunt head that is apparently pushed into soil. The rostral may be slightly enlarged but is never hook-shaped or leaf-like; its edges are rounded. In general, this type of burrower lives in relatively wet, forested country. It is this blunt-headed type of burrowing colubrid that has smooth scales, an unvarying number of scale rows along the body, a short tail, a small head, and reduction in the number of head shields.

Various degrees of loss of head scales are found among colubrids. Although one cannot say with precision that at a certain stage in this process burrowing specialization has been achieved, absence of particular head scales occurs with sufficient frequency in blunt-headed, fossorial colubrids to provide a standard for this specialization. The repeated characters are: (1) rounded rostral; (2) no loreal, or no preocular, or neither; and (3) no anterior temporal. In recognizing specialized burrowing colubrids, we have used as criteria number 1 and number 2 or 3. In addition the snakes of this category have: (4) smooth scales, (5) no scale row reductions, and (6) the head not distinct from the neck.

Genera in the Old World tropics meeting these criteria are listed in Table 58. Other blunt-headed genera from these areas may be fossorial or at least secretive but are excluded from the table because they do not meet our criteria and, hence, have not reached the level of specialization of those listed. In the Indo-Malayan area, for example, *Brachyorrhus* is omitted because it has a scale row reduction; *Macrocalamus* and *Oreocalamus* are omitted because they have loreal, preocular, and anterior temporal scales.

The genera in Table 58 are not equally specialized. Some have lost more head scutes than others. Division of these genera into groups can be made on the basis of several of the head-scute characters, e.g., on the basis of presence or absence of the loreal, temporals, or internasals. In all such classifications, the groups represent different levels of specialization, but they may be polyphyletic assemblages resulting from convergence.

If the presence of grooved maxillary teeth and of hypapophyses on the posterior vertebrae are used for grouping genera, an entirely different pattern emerges. Neither of these characters is a necessary correlate (Cain and Harrison, 1960) of characters adapted to fossorial life. They have no functional relation to the burrowing adaptations and do not appear to be related to those adaptations in morphogenetic fields. Grooved maxillary teeth and hypapophyses on posterior vertebrae appear in snakes of diverse habits. Thus these two characters give an independent check on convergence in burrowing adaptations.

All except two of the African genera have grooved maxillary teeth (fangs) and no hypapophyses on the posterior vertebrae (Table 58). This combination of characters is not found in genera from the other two areas. All of the genera from India and Southeast Asia[1] have posterior hypapophyses but no fangs. All but one of the Indo-Malayan genera lack both fangs and posterior hypapophyses. The almost complete geographic separation of the character combinations is strong, presumptive evidence that at least three stocks are involved in the evolution of these burrowing colubrids.

On the basis of the data in Table 58 we think that this assemblage of burrowing snakes is polyphyletic (Fig. 64A) and that the Indo-Malayan genera, except *Oxyrhabdium*, represent one stock of colubrids; that the Indian genera represent a second, with which *Oxyrhabdium* may be associated (see also Leviton, 1957); and that the African genera represent at least one and possibly two more stocks, an opisthoglyphous group characterized by a very low number of maxillary teeth and possibily an aglyphous group made up of *Poecilopholis*[2] and *Stenorhabdium.*

Other interpretations are possible. One could consider all of these genera as forming one monophyletic, burrowing colubrid group that diverged into various genera after it became specialized for burrowing (Fig. 64B–D). A monophyletic group may or may not undergo geographically limited radiations of subgroups.

If geographically limited subgroups are not involved, certain assumptions are implicit. In the first place, the derived characters (that is, those not present in the ancestral stock) of each genus must have been acquired independently. What happened to one genus was independent of changes in the genotypes of all others, particularly if the genotypic change had little to do with improving the fossorial adaptation. Secondly, a series of identical but genetically independent changes took place in the genera of one area while a different series of identical but genetically independent changes occurred in a second area (Fig. 64B). In this particular case, grooved maxillary teeth evolved independently in a number of genera only in Africa, whereas posterior vertebrae having hypapophyses evolved almost exclusively in those representatives of this stock in India and Southeast Asia. As an alternative to the second assumption, one could assume geographically random evolution of certain characters (e.g., grooved maxillary teeth) followed by selective extinction resulting in the geographic segregation now found (Fig. 64C). Either form of the second assumption calls for a kind of strong, local selection that seems most unlikely. Therefore the second assumption has such a low probability of matching the actual events that we reject the possibility of no geographically limited stocks.

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[1] *Calamaria* actually occurs here, but is represented by only 3 of its 50 species. This region is clearly peripheral for *Calamaria.*

[2] The presence of an anterior temporal scale and a divided anal plate in *Poecilopholis* suggest that it is not related to the Indo-Malayan group.

If one branch of a monophyletic burrowing stock radiated in Africa, one in India and southeastern Asia, and another in the Indo-Malayan area (Fig. 64D), the similarities among genera within each area and the differences between genera of different areas are understandable in terms of phylogenetic theory. The designation of separate branches implies genetic divergence that developed either before they appeared in their respective geographic areas or very soon thereafter. In either case the similarities within areas and the differences between areas can be accounted for by this initial genetic divergence.

The differences between the last hypothesis and the first one, namely, that at least three colubrid stocks have converged on the burrowing adaptive zone, is a matter of timing. Did these stocks or their respective antecedents diverge before they entered the burrowing zone or after?

We believe that divergence into at least two groups and probably three took place long before they entered the burrowing zone, primarily because of the distribution of opisthoglyphous genera. Almost half (26 of 58) of the African colubrid genera listed by Boulenger (1910, 1915a, 1915b, 1915c, 1920) have grooved maxillary teeth. More recent revisions do not change the proportion appreciably. Bogert's list (1940) of African colubrids includes 32 opisthoglyphous genera out of 71.

The close relationship of some aglyphous and opisthoglyphous genera, such as of *Hypsiglena* and *Leptodeira* (Duellman, 1958; Leviton and Tanner, 1960) and of *Chrysopelea* and *Dendrophis* (Smith, 1943), and the variation in development of grooves in the maxillary teeth in some genera, such as *Aparallactus* (Bogert, 1940), has led many workers to recognize that the opisthoglyphous condition has arisen a number of times (Bogert, 1940; Smith, 1943). However,

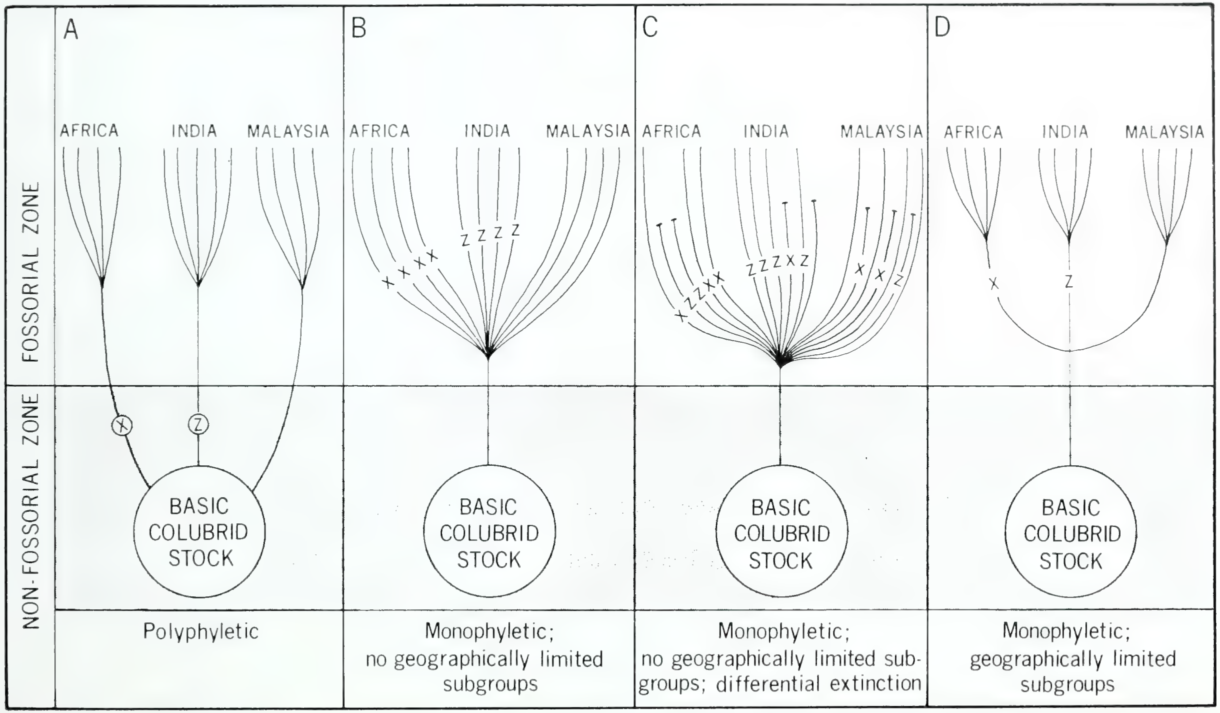
FOSSORIAL ZONE
NON-FOSSORIAL ZONE
A
B
C
D
AFRICA
INDIA
MALAYSIA
X
Z
BASIC COLUBRID STOCK
Polyphyletic
Monophyletic; no geographically limited subgroups
Monophyletic; no geographically limited subgroups; differential extinction
Monophyletic; geographically limited subgroups

FIG. 64. Alternative hypothetical phylogenies of Old World fossorial colubrid genera. Phyla marked with X have rear fangs. Those marked with Z have hypapophyses on posterior vertebrae. Unmarked phyla have neither of preceding characters. Extinct phyla marked with horizontal bar.

no one has suggested that every opisthoglyphous genus represents an independent evolution of grooved maxillary teeth; in fact, such a suggestion would be unreasonable. Probably the African opisthoglyphs represent very few lines of evolution. Bogert's tentative classification has three clusters of opisthoglyphous genera.

The ecological distribution of the African opisthoglyphs suggests adaptive radiation within a continental area similar to that undergone by other vertebrates (e.g., marsupials in Australia). Five of the genera are arboreal, nine terrestrial, fifteen fossorial, and three of unknown habits. One of Bogert's clusters of opisthoglyphs (Groups XIII to XVII) includes five arboreal genera, seven terrestrial, and five fossorial.

Opisthoglyph genera form only 27% (15 of 55) of the total colubrid genera of India and Southeast Asia (Smith, 1943) and only 26% (14 of 54) of the total in the Indo-Malayan area (Smith, 1930; de Haas, 1950). The two halves of the Oriental Region together have only 18 opisthoglyph genera. Ten of the 18 belong to the subfamily Homalopsinae and represent a single line of evolution that probably is not closely related to any other opisthoglyph snakes. The remainder includes two terrestrial genera, *Telescopus* and *Psammophis*, which are widely distributed in Africa and are at best marginal members of the India fauna. Five other genera are arboreal and one is of unknown habits.

We conclude from a comparison of the frequency and ecological distribution of the African and Oriental opisthoglyph colubrids that those of Africa, including the fossorial types, represent the results of the radiation there of one or a very few ancestral stocks. From this conclusion follows our belief that the burrowing genera of Africa and those of the Oriental Region reflect the convergence of at least two colubrid stocks that had diverged prior to their adoption of fossorial habits.

Whether two or three stocks are involved depends on the relations between the Indian and Indo-Malayan genera. If we temporarily exclude *Oxyrhabdium*, the basic difference between these two sets of genera lies in the presence of posterior hypapophyses in those from India and Southeast Asia. Though workers in the past have hesitated to recognize subfamilies on the basis of this character, many have nonetheless been sufficiently impressed by it to use it for delimiting groups of related genera.

Dunn (1928) distinguished subfamilies on the basis of presence or absence of the posterior hypapophyses. Bogert (1940) used the posterior hypapophyses as the basis of the primary dichotomy of

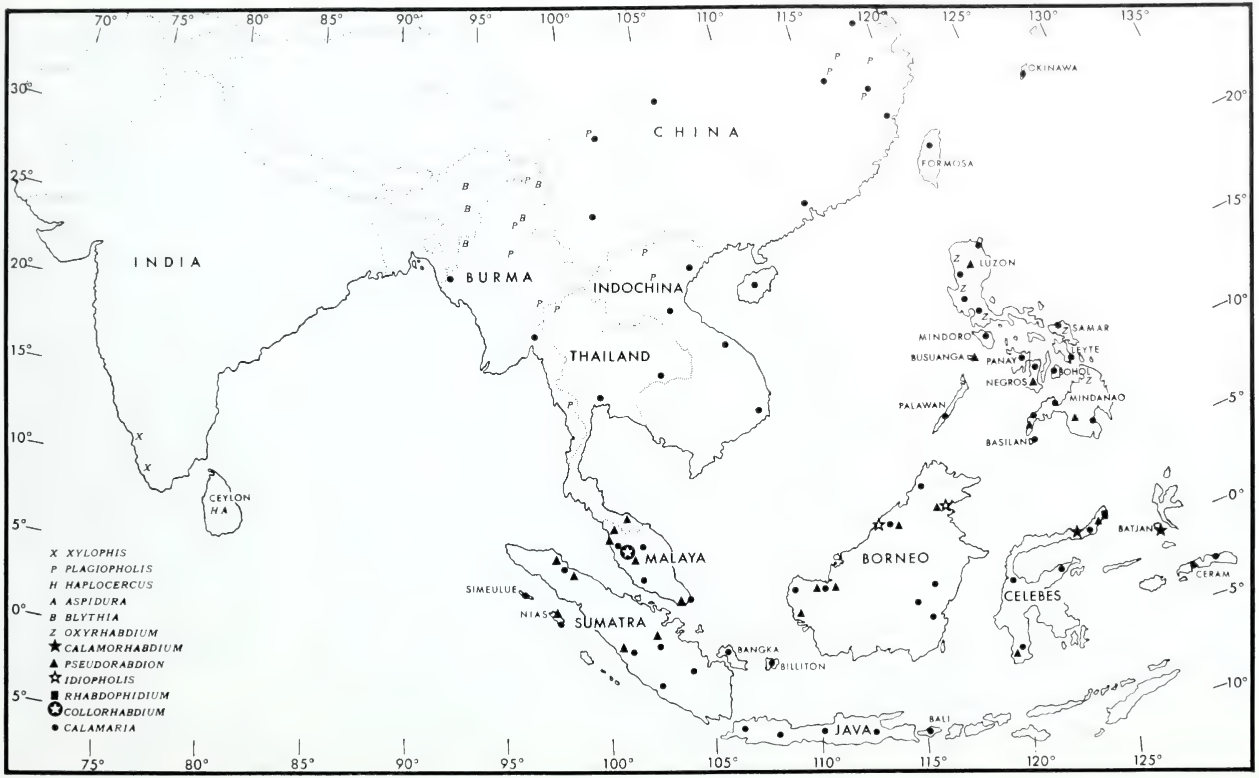

FIG. 65. Distributions of specialized fossorial colubrid genera in Oriental Region. Some of localities of *Calamaria* in Borneo, Sumatra, Java, Malaya, and eastern China omitted.

African colubrid genera, stating that "... if allowance for variation is made, they do characterize more or less natural groups."

Smith (1943), after first stating (p. 28) that the posterior hypapophyses indicate "... stages in evolution, but not necessarily phylogenetic relationship," used the character (p. 138) to relate several genera with *Natrix*. Smith then listed (p. 139) several genera, including *Aspidura, Blythia, Xylophis, Haplocercus,* and *Plagiopholis,* as forming "a degenerate assemblage, perhaps derived from the previous group" (i.e., *Natrix, Pseudoxenodon,* etc.). Phylogeny is clearly implied.

Brongersma's discovery (1938) that hypapophyses may be present or absent in *Chrysopelea* presents the kind of evidence that has weakened confidence in the character. However, occasional intrageneric or even intraspecific variation does not justify our thinking that each occurrence of the character is an instance of independent evolution. We are following Bogert and Smith, among recent workers, in recognizing interrelationship of genera based on the presence of posterior hypapophyses. The genera of India and Southeast Asia having this character are aquatic, terrestrial, or fossorial, suggesting adaptive radiation of a stock of colubrids. We, therefore, consider that the fossorial genera, *Aspidura, Blythia, Plagiopholis, Xylophis,* and *Haplocercus,* which for the sake of convenience, at least, we will refer to as "natricine," represent a stock different from that that gave rise to the Indo-Malayan genera.

Oxyrhabdium is the only specialized burrowing Indo-Malayan genus having posterior hypapophyses. Probably it is related to the Indian genera (Leviton, 1957) and is a member of the same stock. Besides the character of the vertebrae, it resembles the Indian genera in having a narrow anterior temporal, a moderately high number of maxillary teeth and in certain characters of the skull.

The burrowing genera of India and Southeast Asia have distributions that are peripheral geographically or ecologically (Fig. 65). *Aspidura, Haplocercus,* and *Xylophis* are confined to Ceylon or the southern tip of the Indian peninsula. *Blythia* and *Plagiopholis* are confined to the mountainous northeastern fringe of the Oriental Region. *Oxyrhabdium,* the Indo-Malayan genus that appears to be related to the Indian genera, is known only from the Philippine Islands (Fig. 65). Thus, it, too, has a peripheral distribution in the Oriental Region. If we correctly interpret the relations of these natricine genera, as a group they have a disjunct, peripheral distribution.

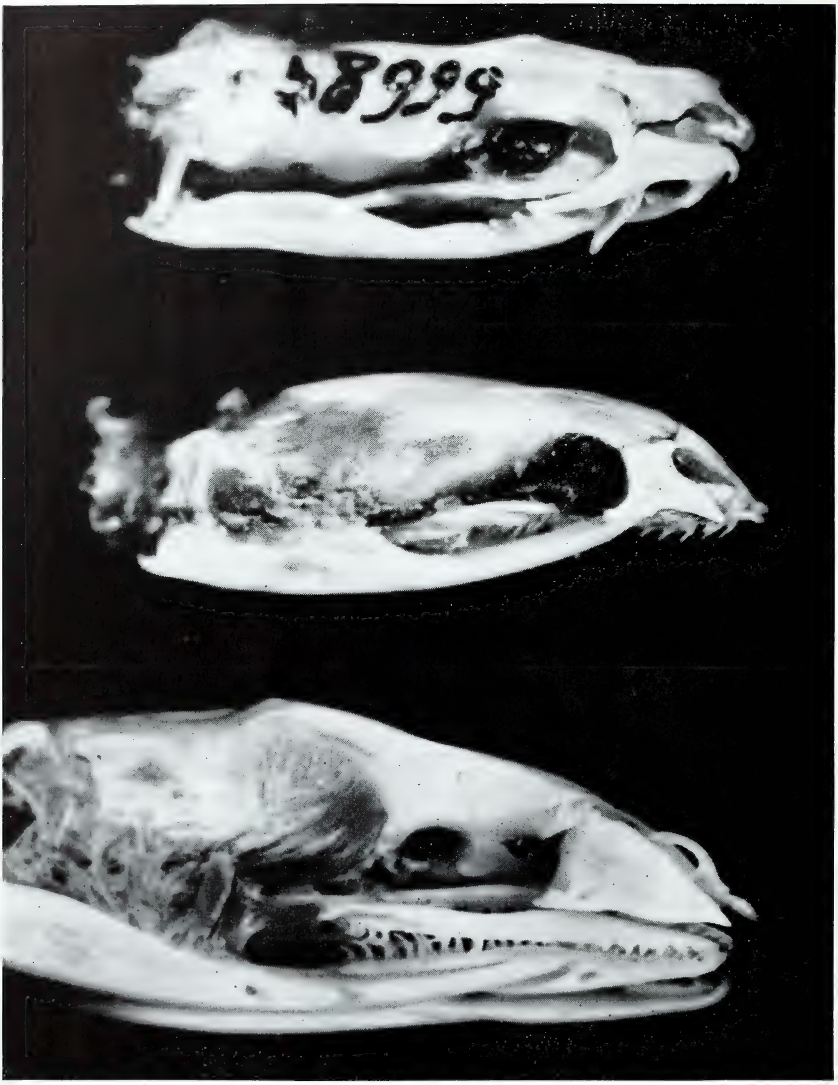

FIG. 66. Skulls of Old World fossorial colubrids showing bones reinforcing side of snout. A. Top, *Miodon gabonensis* (CNHM 58999, length of skull 11 mm.). Middle, *Aspidura trachyprocta* (CNHM 98767, 11 mm.), maxilla and premaxilla missing. Bottom, *Oxyrhabdium modestum* (CNHM 96532, 14 mm.), premaxilla missing.

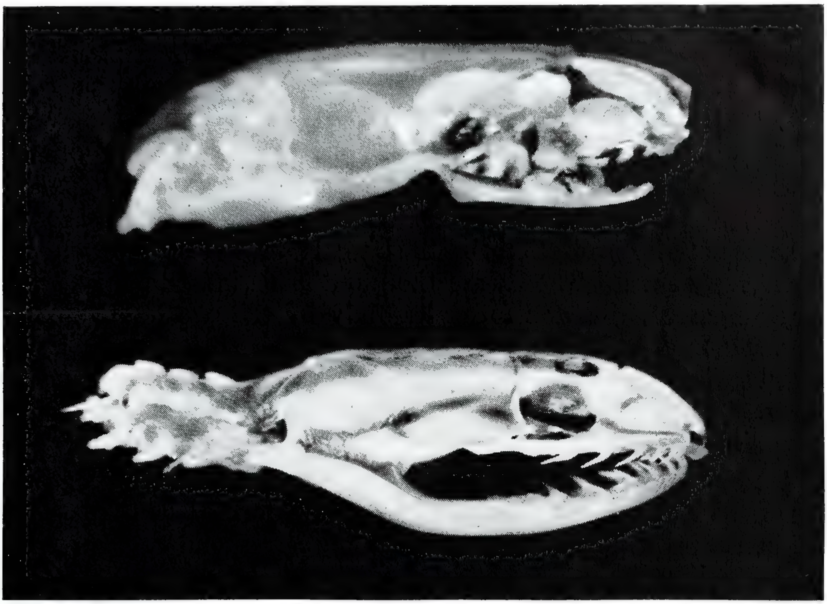

FIG. 66. B. Top, *Calamaria gervaisi* (CNHM 15025, 7 mm.), maxilla displaced. Bottom, *Pseudorabdion longiceps* (CNHM 71596, 8 mm.).

The group comprising the Indo-Malayan burrowing genera (excluding *Oxyrhabdium*), is probably monophyletic or at least formed of closely related stocks. This group, which we will refer to as "calamarine," has a central, continuous range (Fig. 65). The distribution of these two groups of Oriental genera suggests that the calamarines form a relatively recently evolved fossorial group that is more successful and has forced the older, natricine burrowers to the ecological and geographical periphery of the Oriental Region.

The anterior portions of the skulls of these burrowing colubrids support the division into three phylogenetic groups. The lateral surface of the snout in *Calamaria* (Fig. 66B) is protected and strengthened by a bony wall formed by the greatly expanded lateral portion of the septomaxilla (Marx and Inger, 1955, p. 169). The four species of *Calamaria* examined (*gervaisi, leucogaster, schlegeli,* and *septentrionalis*) have squarish prefrontals behind the enlarged septomaxillae. A single skull of *Idiopholis everetti* (CNHM 120377) and one of *Pseudorabdion longiceps* (CNHM 71596) also have squarish prefrontals and expanded septomaxillae forming bony lateral walls to the snouts (Fig. 66B).

In *Aspidura trachyprocta* (CNHM 98767) and *Oxyrhabdium modestum* (CNHM 96532) the lateral portion of the septomaxilla is relatively small, but the prefrontal has a long anterior projection (Fig. 66A) that tends to form a lateral bony wall of the snout.

In the African burrowers, *Calamelaps unicolor* (CNHM 74822), *Chilorhinophis carpenteri* (CNHM 81022), *Miodon gabonensis* (CNHM 58999), and *Aparallactus werneri* (CNHM 81061), the prefrontal lacks an anterior projection and the lateral flange of the septomaxilla is relatively small. The side of the snout has a lateral bony wall of varying extent, the wall formed mainly by the nasal and maxilla (Fig. 66A). The nasal in all of these African snakes has a broad dorsal surface and a ventrally projecting lateral flange at least posteriorly. The maxilla in all four is short and, except in *Aparallactus werneri*, relatively deep and thick.

These burrowing snakes have used three methods of strengthening the side of the snout. The three groups formed on the basis of the bones involved in this strengthening correspond to the groups established on the basis of other characters.

Evolutionary trends within the genus Calamaria.—Analysis of evolutionary trends in the genus *Calamaria* depends on the determination of which characters are primitive and which are advanced or derived. Primitive is used here in the restricted sense of referring to what was typical of the stock from which the genus *Calamaria* arose; derived is applied here to characters that appeared at or after the time the stem of the genus branched off from the rest of the colubrids. This classification of characters can be made only after their distribution in the family Colubridae is analyzed. A trait common to *Calamaria* and most colubrid genera almost certainly was characteristic of the stock from which *Calamaria* evolved; such a character is certainly primitive as we use that term here. A character common to *Cala-*

TABLE 59.—Frequency Distribution of Minimum Number of Supralabials in Indo-Malayan Colubrid Genera.

	Minimum of labials								
Area	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11 or more*	Total
	No. of genera								
East Indies[1]	2	5	6	6	17	6	2	2	46
Malaya[2]	1	4	2	8	9	7	1	0	32

[1] Data from de Rooij (1917) after allowing for uniting *Dendrophis* with *Dendrelaphis* and *Simotes* with *Oligodon*.

[2] Data from Tweedie (1953).

In *Aspidura trachyprocta* (CNHM 98767) and *Oxyrhabdium modestum* (CNHM 96532) the lateral portion of the septomaxilla is relatively small, but the prefrontal has a long anterior projection (Fig. 66A) that tends to form a lateral bony wall of the snout.

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[2] Data from Tweedie (1953).

TABLE 60.—Matrix of Mean Character Differences Among Pairs of Species of *Calamaria* Having Modified Maxillary Teeth.

Species		Species Number																																										
No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1	*lumbricoidea*																																											
2	*griswoldi*	5.1																																										
3	*albiventer*	8.2	6.2																																									
4	*hilleniusi*	7.6	8.6	9.5																																								
5	*muelleri*	16.0	16.6	17.8	20.4																																							
6	*joloensis*	19.2	20.7	19.3	19.6	0.7																																						
7	*bitorques*	13.8	12.1	11.9	16.1	6.9	6.0																																					
8	*gervaisi*	18.4	18.1	17.7	21.4	9.1	8.2	9.5																																				
9	*brongersmai*	28.3	30.1	28.4	24.8	14.6	12.7	19.7	19.3																																			
10	*suluensis*	29.1	25.6	22.5	30.3	15.5	16.8	15.7	13.2	29.4																																		
11	*prakkei*	33.5	30 8	28.2	35.5	21.5	17.1	20.9	17.6	33.8	8.8																																	
12	*everetti*	38.1	35.5	29.8	32.1	32.2	33.1	26.4	24.5	21.0	19.6	25.5																																
13	*palavanensis*	29.4	29.7	28.9	30.6	25.1	27.3	20.9	16.9	17.9	19.8	22.8	8.0																															
14	*grabowskyi*	27.6	24.7	22.8	27.7	22.4	21.3	18.1	15.0	30.9	12.8	15.5	12.8	13.6																														
15	*modesta*	27.2	29.2	30.8	34.1	22.8	30.6	26.7	22.8	20.3	27.7	31.2	29.3	20.1	30.9																													
16	*lateralis*	21.8	20.0	13.8	18.5	25.8	27.0	25.3	28.9	16.2	30.5	35.6	22.0	23.1	31.3	22.8																												
17	*lumholtzi*	26.8	25.3	24.0	24.2	29.3	28.7	32.9	35.8	19.1	43.7	44.0	37.8	32.0	48.2	25.9	9.4																											
18	*bicolor*	18.9	18.9	16.6	17.4	29.5	34.9	23.3	23.4	22.8	30.5	32.6	18.8	15.2	25.8	22.4	10.9	17.3																										
19	*schlegeli*	26.9	23.6	21.7	29.6	34.6	43.1	30.6	35.7	34.4	40.8	41.5	35.0	31.3	37.6	24.2	19.1	14.4	19.9																									
20	*margaritophora*	33.1	34 2	33.9	28.4	23.1	24 2	23.9	18.2	26.6	22.2	26.5	26.5	24.1	21.4	30.0	39.8	52.9	33.7	46.5																								
21	*nuchalis*	31.5	29.3	32.1	32.8	25.5	30.0	22.3	18.8	35.7	20.6	25.1	30.7	25.8	24.2	32.5	44.7	56.9	36.2	42.8	10.6																							
22	*crassa*	18.5	22.2	24.2	22.2	16.4	19 0	14 3	20 4	27.8	28.8	32.2	37.6	31.4	29.6	27.3	36.8	47.7	32.4	33.4	18.1	13.7																						
23	*iselti*	28.1	29.5	29.4	28.2	25.2	19.9	21.7	26.4	32.7	34.2	38.7	43.4	39.9	38.2	39.0	42.0	46.3	41.0	42.8	24.1	14.1	11.7																					
24	*doderleini*	34.0	37.4	41.4	34.3	30.3	29.7	28.1	33.7	20.1	46.4	46.8	33.0	27.2	45.0	26.9	34.4	36.1	32.8	29.7	27.9	25.0	11.6	12.4																				
25	*abstrusa*	14.2	17.6	14.1	18.8	21.4	25.7	21.7	23.9	31.5	32.8	37.2	43.5	40.5	35.8	26.3	25.3	32.1	27.5	27.3	23.5	22.6	12.6	19.6	27.6																			
26	*boesemani*	26.6	28.0	26.7	26.9	37.8	37.1	35.6	41.1	27.6	53.9	54.2	40.4	34.7	52.4	24.3	19.7	21.3	20.0	17.1	35.3	37.3	26.3	27.2	14.8	12.8																		
27	*sumatrana*	40.4	41 2	41.4	44.2	26.2	36 6	30 1	23.7	39.0	26.4	32.4	40.5	34.0	31.6	33.9	36.6	65.2	46.8	51 8	15.6	17.5	24.7	30.8	40.2	29.5	47.7																	
28	*virgulata*	33.8	34.5	37.1	40.4	26.9	32.8	26.9	21.1	28.8	26.2	30.7	28.5	19.9	26.4	23.9	46.6	50.3	35.1	39.2	23.1	19.5	27.7	35.9	32.7	32.8	40.1	17.8																
29	*forcarti*	34.2	32.8	32.8	38.9	23.5	24.6	22.9	28.1	34.8	39.8	33.8	45.9	39.3	34.2	32.9	40.2	51.4	43.9	42.1	28.6	26.2	17.5	24 4	32.0	24.2	39.4	18.7	27.5															
30	*borneensis*	31.7	32.6	33.6	36.7	22.9	29.9	22 8	18.3	37.2	27.1	31.8	39.6	31.4	28.1	26.4	44.4	58.6	37.2	41.7	19.9	21.5	18.2	29.1	33.3	23.8	40.8	24.5	28.8	26 6														
31	*melanota*	29.8	32.6	28 3	33.0	22.8	25.6	21.3	24.0	33.5	32.8	35.5	40.9	35.7	33.5	34.5	39 5	54.2	40.3	40 9	23.8	24.5	13.8	21.5	26.8	18.4	34.2	31.1	34.3	24.7	7.9													
32	*linnaei*	31.1	33 5	34 3	33 4	26 6	30.7	25.7	30.9	34.4	37 3	42.5	48.3	45.5	43.8	43.1	46.9	59.3	46.6	46.1	27.9	19.3	14.1	15.4	23.2	21.6	38.0	30.8	37.6	28.5	16.9	8.8												
33	*javanica*	39.6	41.4	41.2	40.1	39.3	36 0	31.8	32.0	35.6	44.8	49.3	51.7	44.6	42.2	43.6	47.8	53.6	51.1	47.2	18.4	33.6	26.5	31.1	39.7	30.4	48.2	37.4	42.8	34.5	18.5	15.5	17.7											
34	*buchi*	32.2	37.0	34.4	35.1	21.9	22.7	22.2	24.6	32.2	39.4	39.8	48.2	38.8	35.5	46.9	49.7	51.3	48.3	52.8	42.2	45.1	33.3	38.4	44.8	41.4	52.2	41.7	31.6	36 1	25.0	19.3	27.4	31.1										
35	*pavimentata*	36.2	46.5	45.2	49.2	35.2	48.2	35.2	30.8	31.5	40.5	45.0	36.6	29.8	42.8	24.4	41.5	54.7	35.2	41 8	38.5	39.3	36.4	44.9	39.2	41 2	46.7	27.2	24.9	31.2	22.1	27.2	30.3	36.8	30.0									
36	*septentrionalis*	44.6	52.9	56.5	55.1	38.9	54.7	41.9	38.4	35.6	39.9	45.9	40.2	32.9	44.5	30.0	50.2	61.1	43.6	50 4	20.3	29.2	36.0	42.0	38.3	43.2	45.8	25.2	24.7	37.2	21.6	30.8	29.1	35.2	38.1	18.9								
37	*lowi*	38.9	40.1	41.3	45.4	45.0	61.0	45.8	49.1	51.1	60 5	66.5	64.2	53.9	60.3	42.6	47.6	45.2	47.1	35.7	51.2	49.8	41.1	50.5	49.3	31 4	40.6	43.9	39 9	42.2	35.1	32.7	37 2	25.3	37.6	36.8	37.9							
38	*gracillima*	49.8	52 7	57 0	48 0	65.1	74.8	47 8	65.8	52.8	78.3	83.1	64.7	60.7	74.0	55.5	50.7	47.9	50.4	45 9	65.8	62 5	53.7	58 2	45.1	48.6	37 7	57.0	55.9	52 6	52.0	48.1	45.0	35.0	55.2	39.9	46.8	22.5						
39	*rebentischi*	58.1	60.9	59 6	59.8	39.6	40.2	46.2	37.3	27.6	31.0	28.9	28.9	23.1	39.3	31.9	45.0	35.6	41.8	50 0	42.0	48.0	58.3	60.1	47.7	64.6	55.1	51.9	37.2	65.3	58.8	65.3	68.9	52.4	58.4	52.9	44.0	65.0	69.0					
40	*ceramensis*	38.2	41.6	40.2	41.9	27.5	34.8	31.4	26.2	23.7	24.4	25.5	21.3	16.2	25.9	23.0	31.0	30.1	26.4	35 1	31.3	36.2	38.1	48.3	42.2	44 5	49.7	40.1	30.7	45.8	39.1	43.5	51.1	39.2	52.7	37 3	36.6	50.4	58 6	5 2				
41	*mecheli*	52.3	55.8	51.5	51.6	43.8	55.1	44.5	38.7	36.0	40.3	43.4	32.7	27.3	40.3	30.8	45.9	50.4	39.6	41.0	29.1	28 6	33.5	41.0	35.2	38.6	42 7	27.9	24.1	36.5	38.0	39.5	43.9	35.8	57.1	32.4	23.6	37.7	46.8	23 6	17 8			
42	*alidae*	36.8	47.4	47.4	51.6	37.2	41 4	36.5	34 8	42.8	42.7	47.6	45.1	37.4	43.8	32.5	52.3	50.9	44.0	41.4	35.2	34.4	30.1	40.0	33.2	37.3	40 7	27.2	22.6	31.6	31.8	36.9	40.0	32.2	41.9	35.1	35.7	23.3	45.2	36.7	32.2	21.1		
43	*apraeocularis*	35.3	36 5	38.5	41.3	24.2	26 9	26.5	29 1	35.5	39.8	45.8	52.9	44.9	42.5	37.6	49.2	44.9	51.5	41.2	28.4	27.2	20.4	25.1	29.2	25 2	36.7	28.8	32.5	27.3	29.5	38.2	25.4	18.0	40.2	47.1	41.7	28.8	49.3	40.7	38.1	29.5	17.1	
44	*battersbyi*	34.8	50.4	48.9	49.1	51.4	52.1	58 9	55.1	62.9	58.5	58.9	76.9	70.4	63.6	51.8	57.5	59.4	60.1	63.1	41.6	48.4	47.5	49.5	60.5	29.6	43.9	27.8	48.8	29.8	29.3	30.4	31.4	40.9	35.9	35.1	34.4	30.0	34.8	80.6	77.0	59 9	54.4	53.1
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43

maria and other calamarine genera may have appeared in the stock prior to the divergence of *Calamaria,* in which case it is primitive. Or it may have appeared as or after *Calamaria* diverged from a non-burrowing or a less modified burrowing stock, in which case the character is derived.

The calamarine genera of Oriental colubrids may represent several invasions of the fossorial zone by a single stock, or one invasion followed by radiation. Our present information does not permit us to decide which alternative is most likely. The agreement of these genera in the undivided anal and in lack of temporals and scale-row reduction may result from parallel development of different branches of an ancestral non-burrowing stock or from their descent from a common burrowing stock. Whichever is true, these characters are specialized relative to the condition found in other aglyphous, non-natricine colubrids. Because we cannot distinguish between the two possible patterns of evolution of these fossorial genera, we cannot say that these characters in *Calamaria* represent advances of the genus relative to its immediate ancestors.

However, we can speak with greater assurance about certain other characters of *Calamaria.* The fusion of internasals and prefrontals is duplicated only in *Calamorhabdium* among these Oriental genera. If *Calamorhabdium* is closely related to *Calamaria,* this character of the head scales represents an advance or specialization at the time these two genera split off from the remainder of the group. If they are not closely related, this character in *Calamaria* is advanced relative to its immediate ancestral stock and the similarity to *Calamorhabdium* is a product of parallel development.

None of the other calamarine fossorial genera has as few scale rows as *Calamaria.* The possession of 13 scale rows is, therefore, a derived character of *Calamaria* regardless of the pattern of evolution of these fossorial genera. Similarly, the uniquely modified maxillary teeth and the associated deepening of the maxilla are derived characters of *Calamaria.* The last two characters, which we believe are part of a single development unit, are more recent in appearance than either the reduction to 13 scale rows or the fusion of internasals and prefrontals, for otherwise probably all species of *Calamaria* would have the modified teeth barring reversal of evolution.

Reduction of the number of supralabials to five or less is typical of the calamarine genera (Table 58) though rare in non-fossorial colubrids. The seven East Indian genera having such low counts (Table 59) include *Tetralepis,* two homalopsine genera (*Fordonia* and *Can-*

toria), and four calamarine genera. Malayan genera having five or fewer supralabials (Table 59) include three calamarines and the same two homalopsines. The low supralabial counts of the calamarine burrowers, then, probably represent an advance beyond the condition presumably occurring in the ancestral stock. The reduction to five supralabials probably took place before *Calamaria* split off from the remaining calamarines.

The reduction to four supralabials, however, almost certainly took place after *Calamaria* branched off. To assume that the earliest *Calamaria* had four supralabials would oblige one to consider as advanced or specialized certain species (e.g., *C. lumbricoidea*) that on all grounds are among the most similar to other genera of calamarine burrowers. Furthermore, one would be obliged to assume that the course of evolution had been reversed, that instead of continuing the process of consolidation and fusion of head shields that characterizes the entire calamarine group, the genus *Calamaria* had begun to split and increase the number of head shields. Such a reversal would run contrary to what appears to be the most reasonable interpretation of selection pressure, that is, toward increasing refinement of the fossorial adaptation. Consequently, we consider that the earliest species of *Calamaria* had five supralabials and that later the number was reduced to four in several subdivisions of the genus.

Preoculars are sporadic in their appearance in the calamarine genera. Since most colubrid genera have preoculars, probably the ancestral stock of the calamarines did also. As the various calamarine genera split off from that stock several of them—*Idiopholis* and *Calamorhabdium*—lost their preoculars. The others retained preoculars at least until they became distinct genera. Probably *Calamaria* had preoculars at the time it arose and later several of its branches lost them. The converse argument that *Calamaria* originally had no preoculars and then developed them forces one to assume reversal of evolutionary trends, as in the case of the supralabials and with the same unlikely consequences.

The mental scale, which is separated from the anterior chin shields by the first infralabials in the great majority of colubrids, may touch the chin shields or not in the calamarine genera. In *Calamaria* and *Pseudorabdion* both conditions occur. In *Calamorhabdium, Rhabdophidium,* and *Idiopholis* the mental is in broad contact with the chin shields. The most plausible explanation for the distribution of the states of this character is that the ancestral stock of the calamarine burrowers had the mental separated from the chin shields by the first infralabials as in most colubrids and that in certain genera of calamarines the first infralabials became smaller permitting the mental to reach the chin shields. The latter condition, in this view, is the advanced one and its appearance in the calamarine genera is the result of parallelism.

The sequence of appearance of some of these specializations during the phylogeny of *Calamaria* may now be summarized. The loss of anterior temporals, the uniform number of scale rows, the undivided anal, and the reduction in the number of supralabials to 5 or 6 apparently developed early in the phylum leading to *Calamaria.* All of these characters appear in each of the calamarine genera, form important parts (with exception of the single anal) of their fossorial adaptation, and distinguish them from non-specialized colubrids. The reduction of the number of scale rows to 13 and the fusion of the internasals with the prefrontals represent further refinements of the fossorial adaptation that occurred in the stock when *Calamaria* became a distinct genus. At that time, *Calamaria* still had five supralabials, a preocular, and the mental scale separated from the chin shields by the first infralabials.

Shortly after the evolution of *Calamaria* as a distinct group, one of its stocks developed modified maxillary teeth. There are several reasons for believing that this event occurred early in the history of the genus. For one thing, most of the species (44 of 50) have modified teeth. A character appearing before the major radiation of a group is more likely to be found in many species than one appearing later. Other specialized character states—four supralabials, no preocular, mental touching chin shields, eye smaller than eye-mouth distance—occur in smaller proportions of the species (from 9/50 with no preoculars to 27/50 with mental touching chin shields). This criterion for time of evolution assumes no reversal of trends and no multiple, independent origins.

It is possible that any of these structures—teeth, head scales, eyes—may have reversed trends, that a population having five supralabials evolved from one having four, or that a population having a preocular evolved from one lacking a preocular. However, for reasons given above (p. 254) such reversals are unlikely.

Both loss of the preocular and reduction of supralabial counts have probably occurred independently and in various stocks of *Calamaria.* Such extreme reduction of supralabials has taken place in at least five genera of Old World colubrids besides *Calamaria* (*Tetalepis, Oligodon, Chilorhinophis, Amblyodipsas,* and *Xenocalamus*).

Loss of preoculars has also taken place in a number of colubrids (Table 58). Presumably these extreme reductions in head scales do not involve difficult morphogenetic problems and need only the favorable selective pressures of fossorial life in order to become established once the genetic background is available.

Variations in maxillary dentition of colubrids involving number, length, spacing, and grooving of teeth are relatively common. The modification found in *Calamaria,* however, is unique to that genus. Rarity of a character may be caused by unfavorable selective pressure, by difficulties in developmental mechanics,[1] or by rarity of the necessary genetic change. As almost 90% of the species of *Calamaria* have this particular specialization, negative selection pressure seems improbable. The fact that the modification became characteristic of any population suggests that the necessary genetic mutation was recurrent; a gene mutation that occurs only once in a sexually reproducing organism is unlikely to become characteristic of a species (Wright, 1949a). Chromosome mutations, such as autotetraploidy or translocations, may produce reproductively isolated strains from a single event but are uncommon (Wright, 1949b). If a genetic mechanism is rare it is not likely to provide the background for any morphological change whether common or rare. Thus, the most likely explanation for the uniqueness of maxillary teeth modified in this particular way is some difficulty in developmental mechanics.

Almost certainly modification of the maxillary teeth occurred before reduction of supralabial counts to four, loss of the preocular, and establishment of contact between mental and chin shields. All possible combinations of these last three characters are found in the group of species having modified teeth. Hence, if one assumed that change in the supralabials, preocular, or mental scale took place before the change in the teeth, it would follow that modification of teeth had occurred independently in at least two stocks. In view of the rarity of such modified teeth in the family Colubridae, we think it unlikely that they evolved twice in the genus *Calamaria.* Because of repeated development in unrelated colubrids (p. 255), it is far more likely that evolution of the specialized conditions of the other structures mentioned in this paragraph took place independently in various stocks of *Calamaria.*

The times of origin of the derived conditions of other characters are much less clear. Almost all possible combinations of characters exist, thus assuring that most of the specialized states of these characters arose more than once in the genus. Species lacking a preocular may have four (e.g., *lowi*) or five supralabials (*apraeocularis*); they may have the paraparietal surrounded by five (*rebentischi*) or six scales (*alidae*); they may have the mental touching (*javanica*) or separated from the chin shields (*gracillima*). Species having four supralabials may have a preocular (*linnaei*) or not (*lowi*); they may have five (*ceramensis*) or six scales (*mecheli*) around the parietal; they may have moderate subcaudal counts (*melanota* ♂♂ 24.5, ♀♀ 17.6) or very low ones (*septentrionalis* ♂♂ 16.5, ♀♀ 9.1). Analogous combinations can be observed for other characters that vary in the genus. These combinations can be accounted for only on the basis of repeated parallel developments in the several stocks of this genus.

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[1] Including linkage with genes controlling the early development of fundamental structures as, possibly, the heart or brain, and mechanical interference with neighboring developmental fields.

Because of the extensive parallelism and because we cannot find adequate reasons for weighting these characters,[1] we have attempted a phenetic classification based on mean character differences (Cain and Harrison, 1960)[2] of the 44 species having modified teeth. Table 60 presents the matrix of differences for all possible pairs of species. These differences form the basis of the dendrogram (Fig. 67). The relationships shown were established solely on morphological similarity and no phylogenetic relationship is implied.

The higher the level of the connection between species the more similar they are. Below the level of a mean character difference of 25, the connection between groups of species is uncertain. The *margaritophora-doderleini-eiselti-crassa* group might have been connected directly to the *muelleri* and *lumbricoidea* groups instead of being joined first to the *melanota-borneensis-linnaei* group without affecting the level of the lines significantly.

No "safe" level of mean character differences can be defined except arbitrarily. However, we think the ten clusters of species (Table 61) joined by mean character differences of 15 or less merit serious examination because of their internal similarity.

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[1] For purposes of recognizing species' limits, characters were weighted approximately according to the nature and extent of variation within samples (p. 8 ff.). In general, the more a character varied within samples, the less we relied on it as an estimate of reproductive isolation. The same criterion cannot be applied to characters in determining phylogenetic relationships because the questions asked are not the same. In trying to determine species' limits, the main problem is to identify a threshold of genetic divergence. In the case of phylogenetic relationships, what is sought is the pathway (or pathways) by which organisms have changed. Weighting characters according to extent of variation provides a system of estimating a threshold of genetic divergence (reproductive isolation) but does not provide a means of identifying pathways of evolution.

[2] The methods used are presented in detail in Appendix A.

TABLE 61.—Clusters of Species of *Calamaria* Joined by Mean Character Differences of 15 or Less (see Fig. 67).
Groups at m.c.d. < 15

bicolor—Java, Borneo
lateralis—Java, Borneo
lumholtzi—Borneo

lumbricoidea—Malaya, Sumatra, Borneo, Java, Philippine Islands
griswoldi—Borneo
albiventer—Malaya, Sumatra
hilleniusi—Borneo

muelleri—Celebes
joloensis—Sulu Arch.
bitorques—Luzon
gervaisi—Philippine Islands

suluensis—Borneo
prakkei—Singapore, Borneo

grabowskyi—Borneo
everetti—Borneo
palavanensis—Palawan

eiselti—Sumatra
crassa—Sumatra
doderleini—Sumatra

melanota—Borneo
borneensis—Borneo
linnaei—Java, Bangka

rebentischi—Borneo
ceramensis—Ceram, Amboina

boesemani—Celebes
abstrusa—Sumatra, Nias

margaritophora—Sumatra
nuchalis—Celebes

The clusters in Table 61 are of two kinds. One consists of species whose geographic distributions, taken as a group, are coherent. That is, their joint distributions are restricted to one land mass or to several adjacent land masses whose geologic histories have been closely linked.

The *bicolor* group (Fig. 39), for example, is restricted to Sundaland, an area that was one large land mass (Fig. 71) on several occasions during the Pleistocene (Molengraaff and Weber, 1921). Speciation could have occurred during periods of interruption of the land connections. The *lumbricoidea* group occurs in Sundaland and the southern Philippine Islands (Fig. 72); ocean gaps separating the Philippines from Borneo were reduced if not eliminated during the Pleistocene, facilitating dispersal between Borneo and the Philippines. Although no late Tertiary or Quaternary land connections between Celebes and the Philippines are known, the distribution of the *muelleri* group (Fig. 68) can be explained on the basis of radial dispersal of an old stock from Borneo followed by extinction or greater modification of the remnant in Borneo.

The other clusters of species in Table 61 that make "geographical sense" are the *suluensis*, *grabowskyi*, *eiselti*, and *melanota* groups. Because of the conjunction of geographical and morphological evidence, we are inclined to think that the first seven groups in Table 61 represent phylogenetic groups, that the similarity within each of these groups is the result of common descent. They are, in effect, what Cain and Harrison (1960) call patristic groups.

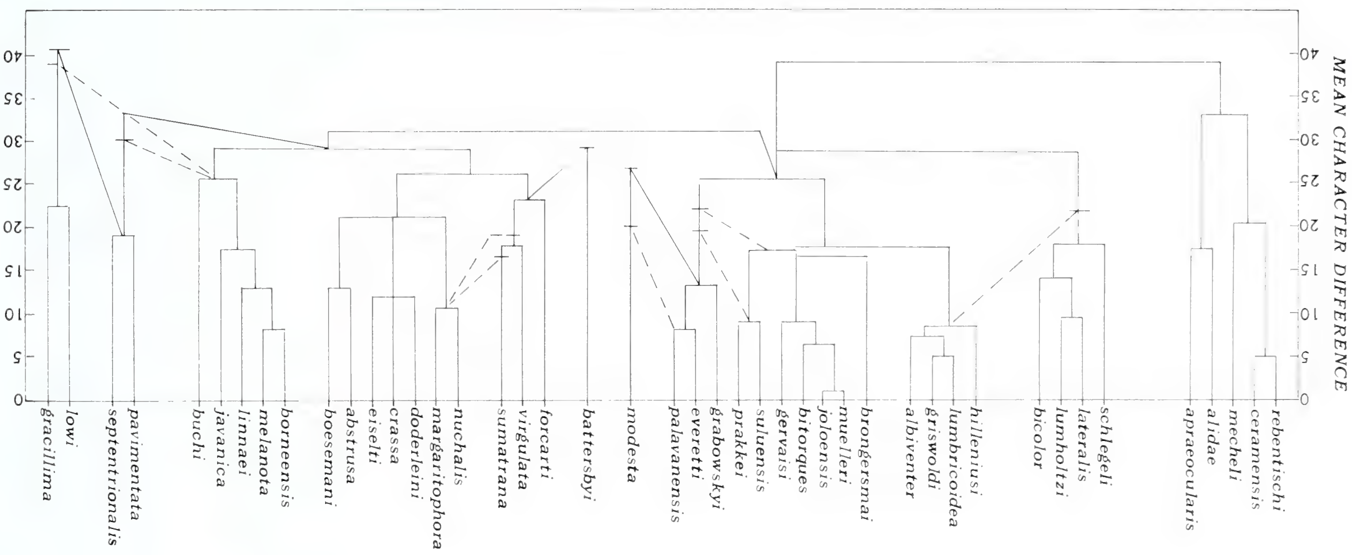

FIG. 67. Phenetic relations among species of *Calamaria* having modified maxillary teeth. Horizontal connections give level of mean character differences of species concerned. Dashed lines indicate alternate connections. Fuller explanation in Appendix A.

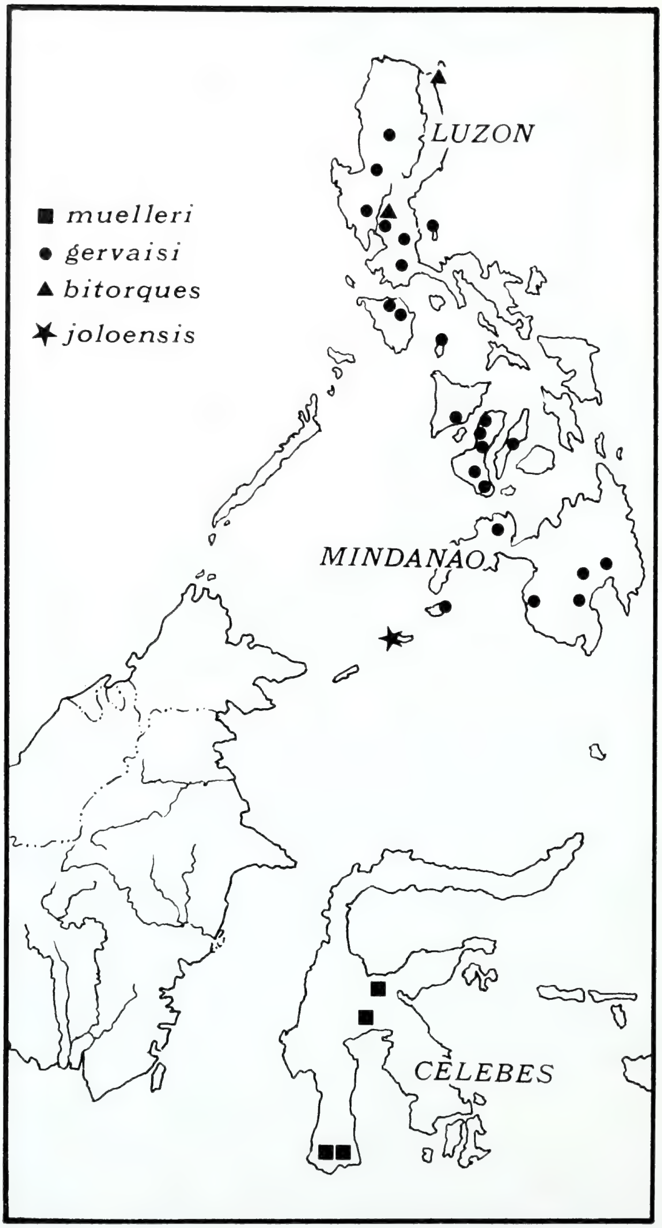

FIG. 68. Distributions of *Calamaria bitorques*, *C. gervaisi*, *C. joloensis*, and *C. muelleri*. Two localities of *gervaisi* and *bitorques* from extreme southeastern Luzon are not shown.

The last three groups in Table 61 have widely disjunct distributions. Although the possibility of extinction of related forms in intervening areas cannot be eliminated, parallelism within a genus of so many forms seems to us to be a more probable explanation of these phenetic assocations. Furthermore, as in two of these groups comparisons were limited to 9 characters instead of the usual 14 we do not have the same degree of confidence in the phenetic resemblance.

Between mean character differences of 15 and 20, species clusters formed are:

schlegeli—Malaya, Sumatra, Borneo, Java
bicolor group—Java, Borneo

javanica—Java, Billiton
melanota group—Java, Borneo, Bangka

pavimentata—Burma, southern China, Indo-China
septentrionalis—eastern China, northern Indo-China

lumbricoidea group
suluensis group
muelleri group

sumatrana—Sumatra
virgulata—Sumatra, Borneo, Java, Celebes, southern Philippines

alidae—Sumatra
apraeocularis—Celebes

The first three of these clusters form coherent geographic units. Probably they are phylogenetic as well as phenetic groups. The fourth in this tabulation, a cluster of groups, is also geographically coherent and is probably a phylogenetic grouping. To this enlarged *lumbricoidea* group the *grabowskyi* group may be added; though the connection is shown by Fig. 67 at a mean character difference of 25, the similarity of the *grabowskyi* and *suluensis* groups, considered alone, is at a higher level as indicated by the dashed line in the dendrogram.

The *alidae-apraeocularis* cluster is disjunct geographically and may represent another case of parallelism. Although *virgulata* and *sumatrana* are similar and have overlapping ranges, we hesitate to call this a patristic group because the taxonomy of *virgulata* is itself uncertain (p. 187).

The highest mean character difference joining species we believe are closely related is 22.5, the level of similarity of *lowi* and *gracillima*.

Several species are not closely related phenetically to any group. *Calamaria modesta* is similar to *palavanensis* at a mean character difference of 20, and to the *grabowskyi* group, of which *palavanensis* is part, at a value of 27. *Calamaria battersbyi*, for which only 8 characters could be used, ties in to the *sumatrana-virgulata* group at a value of 29. *Calamaria buchi* joins the *melanota* group at the level of 25.

The *muelleri* group is apparently the most generalized of those listed in Table 61 and in the tabulation above. The average deviation, calculated from Table 60, of the *muelleri* cluster from all other species is 27.5. The average deviation of other clusters are: *margaritophora*—30.5; *lumbricoidea*—31.1; *eiselti*—31.7; *melanota*—32.0; *boesemani*—32.8; *grabowskyi*—33.4; *sumatrana*—33.4; *suluensis*—34.2; *bicolor*—35.6; *pavimentata*—37.9; *rebentischi*—41.7. The fact that the *muelleri* group has character values closer to the average for these 44 species than any other group does not prove that it is the stem group from which others arose. We think it far more likely that the *lumbricoidea* group represents the stem population because it occupies the heart of the generic range, it is not specialized (see low average deviation, above), and its variability demonstrates that the genetic possibilities for speciation are present. These topics are expanded below.

Mean character differences were calculated for the six species having unmodified maxillary teeth, using the same characters and the same procedures (Table 62). Only *C. leucogaster* and *ulmeri* are closely similar to one another.

None of the species having four supralabials forms part of a cluster with species having five supralabials. These more specialized species form three separate groups (shown at the right of Fig. 67) that join one another at high mean character differences (30). The measure of phenetic resemblance thus seems to bear out our statement (p. 257) that supralabial counts were reduced to four independently in several lines.

There is also a strong tendency for species having the paraparietal surrounded by six scales to form clusters from which those having five scales around the paraparietal are excluded. For example, in Table 61 the sixth, seventh, ninth, and tenth clusters consist of species having the paraparietal surrounded by six scales; those in the other groups all have paraparietals encircled by five scales. Some of the clusters of species on p. 261 have one state or the other of this character, but several of the species in other clusters (e.g., *pavimentata, schlegeli, virgulata*) are variable in this respect.

Sharp dichotomies among species are not based on any other character. Species lacking a preocular (e.g., *javanica*) may form part of a cluster with species having preoculars. Species having the mental shield touching the anterior chin shields (e.g., *grabowskyi*) may form a cluster with species having the mental and chin shields separated.

The clusters of similar species do not show consistent associations of characters that are not necessary correlates (cf. Tables 61, 64). For example, the *lumbricoidea, muelleri,* and *suluensis* groups have five supralabials; only the last two have reticulate patterns in the dorsal scales, and only the last has a light, dark-edged stripe on the first scale row (Table 64). The *lumbricoidea* and *melanota* groups are alike in the presence of preoculars and in the relation of mental and chin shields but differ in supralabial counts and pattern of dorsal scales. Other examples of this nature are apparent from comparison of Tables 61 and 64. This almost exhaustive recombination of characters, to which we have referred above (p. 257), suggests an evolutionary sequence.

Patterns of evolution.—Dobzhansky (1955) cites numerous studies of *Drosophila* showing that many populations, phenotypically rather uniform, in fact carry a large store of genotypic variability. As many as 40 per cent of the chromosomes of some species are heterozygous for deleterious recessives. Ecologically specialized forms of *Drosophila* (e.g., *D. prosaltans*) often have less genotypic variability than their more widely distributed, less specialized relatives (Dobzhansky and Spassky, 1954; Carson, 1959). On the basis of such evidence Dobzhansky suggested the "balance hypothesis" of the origin and maintenance of adaptive norms. According to this hypothesis successful adaptation depends on an array of genotypes heterozygous for gene alleles, gene combinations, and chromosome arrangements.

As an alternative Dobzhansky proposed the "classical hypothesis" which involves the gradual substitution and fixation of favorable mutants. This scheme is at least implicit in much taxonomic literature (e.g., p. 256 of this paper; Gans, 1959, pp. 167–173). According

TABLE 62.—Matrix of Mean Character Differences Among Pairs of Species of *Calamaria* Having Unmodified Maxillary Teeth.

		Species number				
No.	Species	1	2	3	4	5
1	*leucogaster*					
2	*ulmeri*	9.6				
3	*lautensis*	30.1	29.6			
4	*curta*	48.6	35.8	41.0		
5	*acutirostris*	53.6	37.5	46.6	33.9	
6	*schmidti*	47.0	62.5	60.4	52.8	55.6

to this hypothesis, most individuals will be homozygous for most loci and most chromosome arrangements. Carson (1959) suggests this is a common result of homoselection in specialized marginal populations.

The success of the "balance" system involves more than heterotic effects in individuals. Wright's (1949b) model of adaptive peaks of successful gene combinations to which the gene pools of populations return after temporary disturbance or relaxation of selection pressure is predicated on heterozygosity in an organized species system. This heterozygous system has the capacity to withstand temporary changes in the environment without destruction of the basic adaptations and thus has genetic homeostasis (Lerner, 1954).

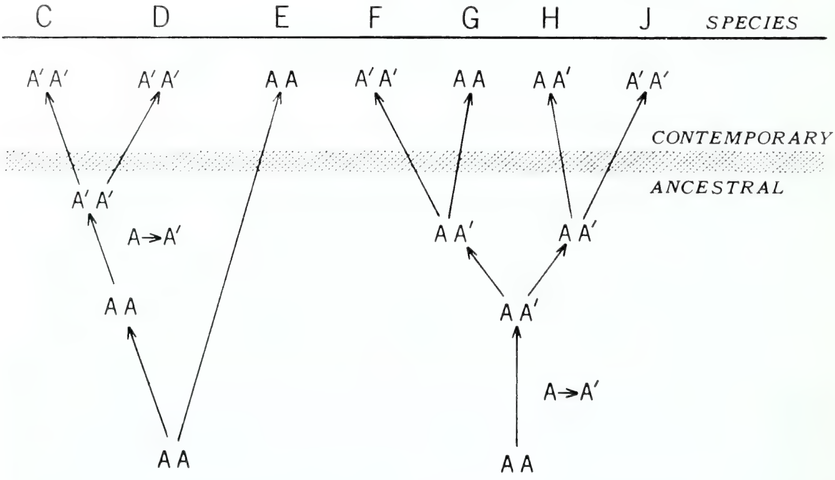

Fig. 69. "Classical" (left) and "balance" hypotheses (right) applied to one locus. Each bifurcation represents development of reproductive isolation. See text for fuller explanation. (After Throckmorton, 1962.)

Throckmorton (1962) outlines a phylogeny in *Drosophila* based on the "balance hypothesis." A heterozygous stem population gives rise to populations that express completely all of the possibilities for diversification (Fig. 69). Under this hypothesis it is possible for two species that have identical genetic compositions, at least at this particular locus, to be derived from separate populations unlike either. By extending the diagram (as in Fig. 70) so that it includes another locus that, for the sake of discussion, modifies a second character, one may arrive at a set of species expressing most of the possible combinations of states of these two characters.

The two contemporary species, K and N (Fig. 70), having identical combinations of these characters are not derivatives of the same ancestral population. In fact, each is more closely related phylogenetically to species having different combinations of states of these characters. The similarity of K and N is the result of parallelism, which we believe accounts for many of the similarities between species of *Calamaria* in particular characters and occasionally in several characters.

This outline, if it does in fact describe the phylogenetic history of any group, depends on the existence for some time of populations having heterozygous genotypes. Have such populations existed in the genus *Calamaria?* At the very least such species populations exist now. *Calamaria lumbricoidea* is the best example. It is variable over narrow or wide geographic areas in dorsal and ventral coloration, type of hemipenis, number of gulars, position of reduction on the tail, ventral and subcaudal counts, and in ontogenesis of dorsal pigmentation (pp. 82 ff.). Two related species, *griswoldi* and *albiventer,* have modifications of the dorsal striping found in some populations of *lumbricoidea.* A third related species, *hilleniusi,* lacks stripes but may have yellow transverse bars, which are found in the young of most populations of *lumbricoidea.* Subcaudal counts are low in *gris-*

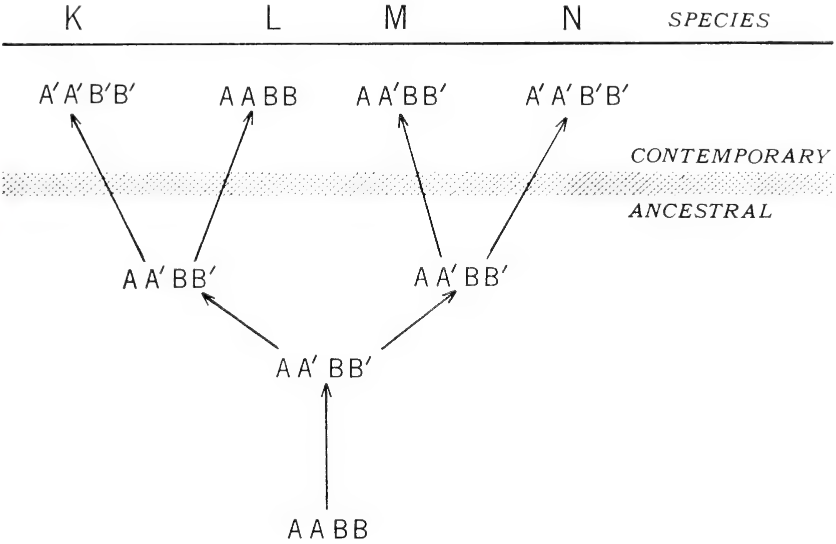

FIG. 70. Balance hypothesis applied to two loci. See text for explanation.

woldi, moderate in *albiventer;* ventral counts are low in *albiventer,* moderate to high in *griswoldi.* Reduction of the dorsal scales on the tail in *albiventer* occurs in the middle and in *griswoldi* in the upper part of the range of variation of *lumbricoidea.*

We are far from certain that *lumbricoidea* (or its antecedent population) is in fact the ancestor of *albiventer, griswoldi,* and *hilleniusi.*

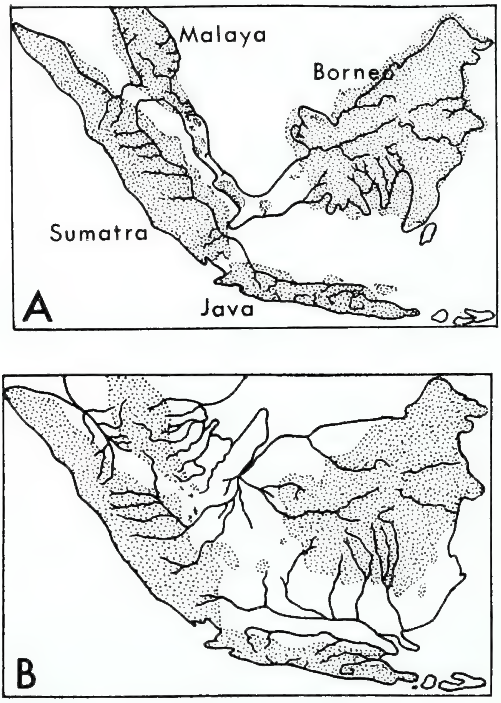

FIG. 71. Pleistocene relations of land areas (after Smit-Sibinga *in* de Beaufort, 1951). Present land areas stippled. Pleistocene coast lines and inland drainages indicated by solid lines. A. First interglacial period. B. Last glacial period.

However, such a relationship is a distinct possibility, for *lumbricoidea* does have a great store of variability and its geographic range spans those of the other three. During the Pleistocene when the area of Sundaland was being fragmented and reunited at intervals (Fig. 71; see also below), a variable population could have split off geographically isolated fragments in which certain variations became fixed either because of inbreeding and random phenomena such as accidents of sampling or because of strong selection for homozygosity (Carson, 1959).

Wright (1932) has concluded that ". . . evolution depends on a certain balance among its factors. There must be gene mutation, but an excessive rate gives an array of freaks, not evolution; there must be selection but too severe a process destroys the field of variability and thus the basis for further advance; prevalence of local inbreeding within a species has extremely important evolutionary consequences but too close inbreeding leads merely to extinction. A certain amount of crossbreeding is favorable but not too much."[1]

Almost all these requirements are satisfied by *lumbricoidea*. Although we know nothing about its genotype directly, phenotypic variation within demes in ventral and subcaudal counts (Table 23) and in coloration (Tables 21, 22) is strong evidence of genotypic variation. The prevalence of one type of dorsal coloration over wide areas shows that, despite some variation, mutation has not run wild. The narrow range of ventral counts within and the differences between local populations (Tables 23, 24) indicate that local inbreeding has taken place. Yet the wide geographic range of particular dorsal patterns is evidence that some crossbreeding has also occurred.

The events of speciation in the *lumbricoidea* group (Fig. 72) can be visualized along the following lines. In one fragment (*albiventer*), isolated in Malaya during a period of high sea levels, a uniformly light venter became fixed, dorsal striping of one sort became constant, ventral counts were restricted to a low range and subcaudal counts to a moderate one. Possibly in the same interval a fragment (*griswoldi*), isolated in northern Borneo, lost all trace of dark ventral bars, the dorsal pattern of light lines became fixed, ventral counts became restricted to high levels and subcaudal counts to low ones.

At the same time the remainder of the species population in Sumatra retained most of its original variability in these characters. Dorsal striping between all adjacent scale rows may have been characteristic of the Sumatran population at this time.

Then when continuity between land masses was re-established during the next eustatic lowering of sea level, the Malayan isolate, now a reproductively isolated species, spread westward into Sumatra. The northern Bornean isolate apparently had become specifically adapted to moderately high elevations, a type of specialization Carson (1959) visualizes as one of the consequences of homoselection and and random drift in small marginal populations. Such a specializa-

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[1] Although the statement quoted is 30 years old, the idea of a balance among forces is still widely held, as can be seen in Wright (1955), and in Mayr's (1963, p. 2) analysis of the "synthetic theory" of evolution.

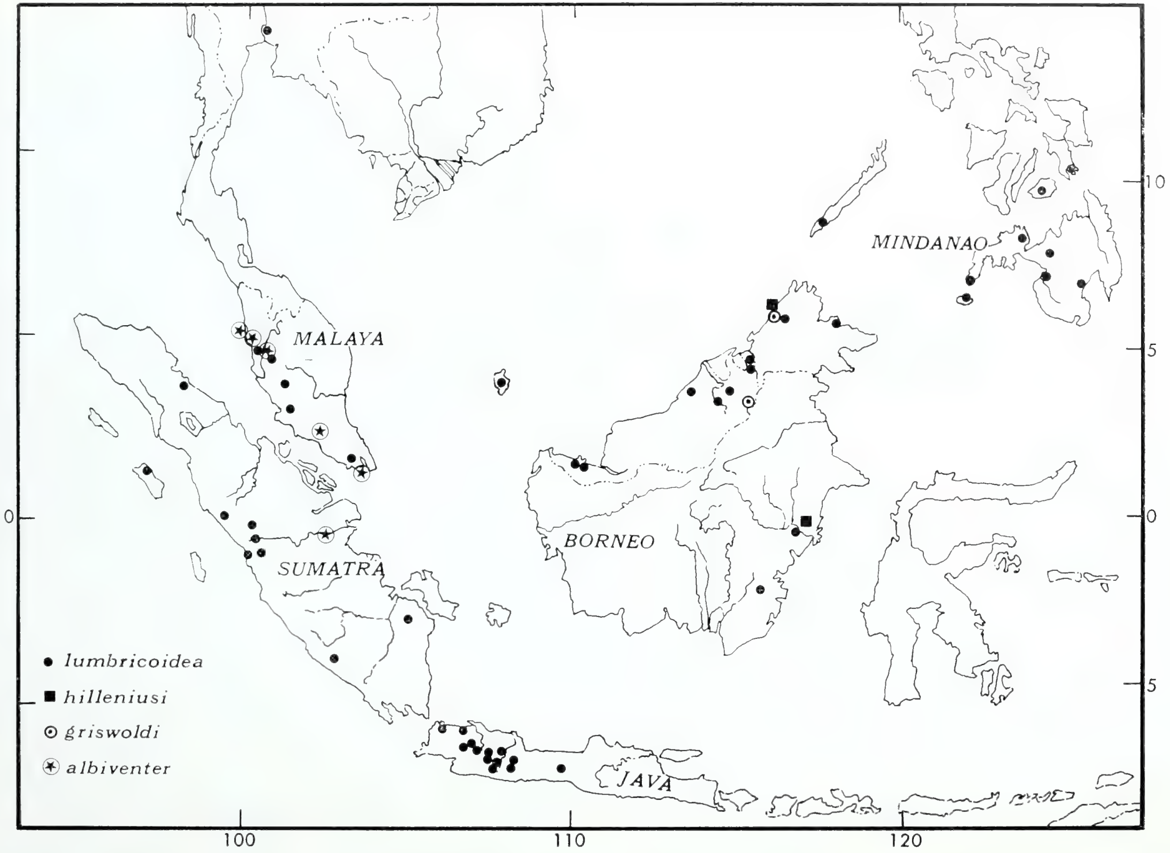

FIG. 72. Distributions of *Calamaria albiventer*, *C. griswoldi*, *C. hilleniusi*, and *C. lumbricoidea*.

tion could have prevented the dispersal of *griswoldi* through the lowlands of the newly re-formed Sundaland. The striped but otherwise variable Sumatran population at this time spread eastward into Malaya, into Borneo and Java, and probably even reached the Philippine Islands.

When these populations were isolated from one another during the next rise in sea level, a new, more vigorous epigenotype, having as one of its phenotypic manifestations a uniform dark dorsum in adults, gradually replaced the old, "striped" *lumbricoidea* genotype in Borneo. Following the next lowering of sea level and the subsequent reunion of Sundaland, this new vigorous genotype spread into eastern Sumatra, slowly replacing the "striped" genotype until the latter became restricted to the western fringes of Sumatra. The new genotype also reached the lowlands of western Malaya and similarly replaced the striped variant until the latter came to be restricted to its present range in the mountains of central Malaya. The genotype associated with uniform dorsal coloration may have spread to Java at this time or the phenotype may have developed there independently. Apparently, this genotype did not reach the Philippines. Thus, the new, more vigorous genotype in some areas replaced the older one completely and in others pushed the older one to the geographical or ecological limits of the species range.

During the interval of land fragmentation following the Pleistocene, differentiation has continued. Yellow dorsal rings and dark ventral bars have been lost in scattered populations (p. 82), and the ranges of variation of ventrals and subcaudals have continued to differentiate from population to population.

On the basis of the few specimens known, speculation concerning *C. hilleniusi* is perhaps not justified though it is tempting to suggest that its history parallels that of *griswoldi*.

This picture of speciation in the *lumbricoidea* group may be oversimplified; it is certainly speculative. Nevertheless, it fits the known Pleistocene history of Sundaland (Molengraaff and Weber, 1921; de Beaufort, 1951). It also resembles closely Wright's theoretical picture of the population structure most likely to evolve continuously (Wright, 1949a, pp. 381–382): a species population consisting of semi-isolated local populations in which the varying effects of local selection and inbreeding may produce new favorable gene combinations that will spread through adjacent demes as opportunity presents itself only to be replaced by later, still more favorable combinations. In several of the postulated local populations that became geographically isolated temporarily, local selection or inbreeding carried the process of differentiation too far. These populations became reproductively isolated, recognizably distinct species (*albiventer*, *griswoldi*, and, probably, *hilleniusi*). Their internal uniformity has effectively cut them off from the continuing process of evolutionary advance of which the parent population, *lumbricoidea*, still seems capable.

The evolutionary potential of *lumbricoidea* is probably not confined to speciation, that is, to the production of new species that are morphologically distinct but essentially in the same adaptive mold. *Calamaria lumbricoidea* is generalized enough that it could evolve in any number of adaptive directions. It could, for example, become more slender and shorter-tailed and, hence, approach the form of *virgulata*. It could reduce the number of supralabials, shorten the tail, and thus develop in the direction of the form of *Calamaria septentrionalis*.

Calamaria schlegeli may be another species that, like *lumbricoidea*, has been evolving actively and providing the source of other, reproductively isolated, populations. Like *lumbricoidea*, *schlegeli* has an extensive geographic range encompassing those of the postulated offshoots and morphological variability that can be arranged hierarchically from local individual to macro-geographic variation.

The preocular scale (p. 155, Tables 42, 43) may be present or absent in a geographically restricted sample (e.g., western Sumatra), and when present in such a sample it may be large or small. The variation of the preocular may also be severely limited over a wide geographic range, as in Java. The same patterns of variation appear in head coloration (Table 44). Ventral and subcaudal counts, however, vary from deme to deme but show no macro-geographic patterns (Table 45).

Thus observed variation in *schlegeli* can be interpreted as the result of a combination of moderate local inbreeding, gene flow, selection, and mutation or recombination—the same combination that we have suggested makes the continued evolution of *lumbricoidea* very likely. The species in the *bicolor* cluster (Table 61) probably are branches from the *schlegeli* stock.

Calamaria pavimentata is also subject to local differentiation and individual variation (pp. 215 ff.), the latter in elements of coloration and the former in ventral and subcaudal counts (Table 54). However, what this wide-ranging species lacks that *lumbricoidea* and *schlegeli* have is variation at the macro-geographic level. Possibly the largely continental range of *pavimentata* has not provided the same opportunities for temporary geographic isolation enjoyed by populations of *Calamaria lumbricoidea* and *schlegeli* in their largely insular ranges.

Another factor that may inhibit the evolution of *pavimentata* is the environment. The range of this species is close to what is probably the ecological limits of the genus (see below). Although Mayr (1963, p. 546) seems to believe that isolated populations at the ecological boundary of a species range represent the situation having the greatest opportunity for "adaptive shifts and evolutionary novelties," the species frequency distribution of *Calamaria* (pp. 272 ff.) suggests the opposite, that the greatest opportunities for this group have been in the center of the generic range.

The insular species *gervaisi* shows individual variation, local differentiation, and macro-geographic variation. Because variation in *gervaisi* is limited to ventral and subcaudal counts and to minor aspects of coloration, it seems to lack the potentiality for evolution seen in *lumbricoidea*. Nevertheless, an old isolate from *gervaisi* may have developed into the species *bitorques*. Some Luzon specimens of *gervaisi* have two yellow rings on the neck enclosing a darker area (p. 112). Multiplication of these rings, which might have happened in a small, isolated population, would result in the pattern of *bitorques* which has two to six dark saddles separated by yellowish rings. The Philippine archipelago has been unstable geologically, with periods of submergence and fragmentation of land masses alternating with periods of emergence and land connections. Under these circumstances so conducive to speciation, it is surprising that more species of *Calamaria* have not evolved in the Philippine Islands.

The only other species having the characteristics we have come to expect in continuously evolving populations is *lowi*. *Calamaria lowi* has a moderately extensive range from Malaya to Java and Borneo, and varies over narrow or wide areas in the number of supralabials bordering the eye, the extent of spotting on the side of the body, the relation between mental and chin shields, and the numbers of infralabials, ventrals, and subcaudals (pp. 221 ff.). Geographic variation is sufficient for the definition of subspecies. The potentiality for continued evolution of *lowi* is probably more limited than that of the *lumbricoidea* stock, for example, because of its extreme specialization. By virtue of reduction in the orbital region, reduction of supralabial counts, extreme slenderness of the body, and shortness of the tail, *lowi* probably can evolve only in the direction of increasing fossorial specialization. Some of the special adaptations of *lowi*, such as reduction of the orbital region, would have to be reorganized in order to permit *lowi* to evolve along more generalized lines.

The limitation of evolutionary directions does not, however, cut *lowi* off from the usual processes of speciation. Geographic variation in isolated land masses is evident now. If geographic isolation continues long enough, inherent barriers to interbreeding may develop. Probably *gracillima* owes its origin from the *lowi* stock to these processes of geographic variation and isolation.

Distribution.—Although two species of *Calamaria, septentrionalis* and *pavimentata,* occur as far north as 30° N, the genus is essentially tropical with a pronounced center of distribution in Borneo and Sumatra (Fig. 65, Appendix B). Of the 50 species, 21 are known from Borneo and 16 from Sumatra, thus accounting for 64 per cent of the species (five species common to both islands). In all directions from these two islands, the number of species drops off rapidly. The southern Philippine Islands have 5 species, Celebes 8, Java 9, Bali 1, and the Malay Peninsula 6. Four species occur in Indo-China and China, one of them (*pavimentata*) entering Formosa and the Riu Kiu Islands. A single species, *ceramensis,* found in Ceram, represents the southeasternmost extension of the generic range.

The northern and western limits of the range are apparently formed by ecological barriers. Low temperatures probably limit dispersal of *Calamaria* northward and increasing seasonal aridity may inhibit dispersal westward. The ranges of *septentrionalis* and *pavimentata* (Fig. 73) almost coincide with the areas of southeastern Asia having at least 25 cm. of rain in the period November through April.

The southern boundary of the generic range is a geographic barrier. The eastern limits are a combination of ecological and geographical barriers. The area between Celebes and New Guinea has probably been occupied largely by seas throughout the Tertiary and Quaternary (Umbgrove, 1949). Thus a geographical barrier has inhibited the dispersal of *Calamaria* eastward from Celebes, and has allowed only one species, *ceramensis,* to get as far as the Moluccas.

The rapid decrease in species of *Calamaria* eastward from Sumatra in the Sunda chain parallels changes in the distribution of other organisms. Mayr (1945) notes that Sumatra has 440 species of birds, Java 340, Bali 166, and Lombok 119. The decrease is conspicuous in Java itself, for only 245 species of birds occur in the eastern half of the island and probably only 170 reach the eastern tip. The numbers of *Calamaria* in these islands are: Sumatra 16, Java 9, Bali 1, and Lombok 0. Definite localities are available for only five of the Javan species. All five—*modesta, virgulata, lumbricoidea, linnaei,* and *schlegeli*—occur in western Java, only the last three in central Java, and only the last two in eastern Java. *Calamaria schlegeli* is the only species to reach Bali. Mayr (1945) attributes the impoverishment of the bird fauna within Java to the increasing aridity eastward in the island and notes that lowland rain forest is replaced by drier monsoon forest in eastern Java. The same climatic factor could account for the decrease in species of *Calamaria* eastward in Java and for the presence of only one species in Bali. The Lesser Sunda Islands

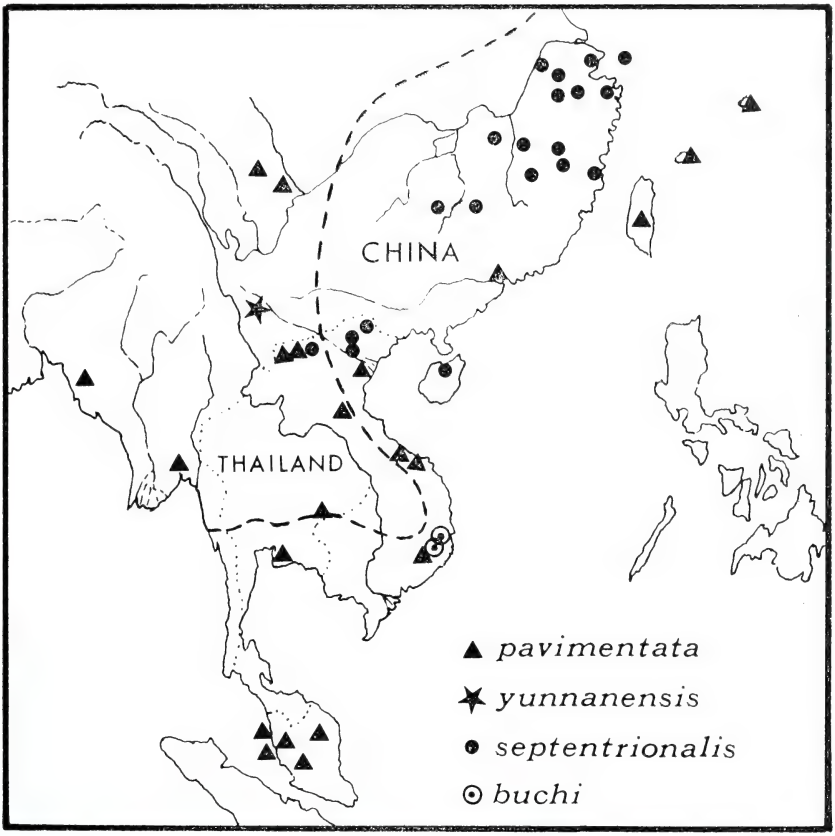

FIG. 73. Distributions of *Calamaria buchi, C. yunnanensis, C. pavimentata,* and *C. septentrionalis.* Dashed line shows northern and western limits of area having at least 25 cm. of rain in the interval Nov. 1–Apr. 30 (after Goode's School Atlas).

TABLE 63.—Geographic Distribution of Principal Morphological Variations of the Genus *Calamaria*.
(Plus sign indicates occurrence, zero absence.)

	Borneo	Sumatra	Java	Malaya	Celebes	Philippine Islands	Indo-China, China
Supralabials 5	+	+	+	+	+	+	0
4	+	0	+	+	0	0	+
Scales around paraparietal 5	+	+	+	+	+	+	+
6	+	+	+	+	+	0	+
Preocular present	+	+	+	+	+	+	+
absent	+	+	+	+	+	0	+
Reduction of dorsal scales > 8.5	+	+	+	+	0	+	0
< 8.5	+	+	+	+	+	+	+
Ventrals > 185	+	+	+	+	+	+	+
< 185	+	+	+	+	+	+	+
Subcaudals > 20	+	+	+	+	+	+	0
< 20	+	+	+	+	+	+	+
Sex dimorphism, ventrals > 15	+	+	+	+	+	+	+
< 15	+	+	0	+	+	+	0
Sex dimorphism, subcaudals > 7	+	+	+	+	+	+	+
< 7	+	+	+	+	+	+	0
Mental and chin shields, touching	+	+	+	+	+	+	+
separated	+	+	+	+	+	+	+
Scales with network	+	+	+	+	+	+	+
without network	+	+	+	+	+	+	0
Light stripe on 1st scale row, present	+	+	+	+	+	+	+
absent	+	+	+	+	+	+	+
Light markings at vent, present	+	+	+	+	+	0	+
absent	+	+	+	+	+	+	+
Teeth > 8.5	+	+	+	+	+	+	+
< 8.5	+	+	+	+	+	+	+
Teeth, modified	+	+	+	+	+	+	+
unmodified	+	+	0	0	+	0	0
Gulars 3	+	+	+	+	+	+	+
4	+	+	+	+	+	0	0

become increasingly arid eastward. The absence of *Calamaria* east of of Bali may result from this climatic deterioration and from the age and depth of the straits between Bali and Lombok.

Centers of evolution and dispersal.—The numbers of species of *Calamaria* occurring in different land masses (Appendix B) are not closely correlated with the sizes of those areas. The parts of China and Indo-China included in the range of *Calamaria* far exceed in size any of the other areas but have very few species. The next two largest areas, Borneo (286,969 square miles) and Sumatra (163,557 square miles), have most of the species. Celebes (69,277 square miles) is considerably larger than Java (48,842 square miles) but has fewer species. The southern Philippine Islands—Mindanao, Jolo, and Palawan—have almost the same area (41,432 square miles) as Java but only half as many species.

Scarcity of species in southern China can be explained on the basis of unfavorable climate (see above). The small number of species in the Philippine Islands cannot, however, be explained in ecological terms as the climate and vegetation are not very different from those of Borneo or Java. For the same reason, the drop in species number in Celebes probably does not have an ecological basis.

If one considers the Tertiary and, especially, the Pleistocene history of the Indo-Australian archipelago, the distribution of species becomes understandable provided one assumes that the centers of evolution and dispersal lie in the Borneo-Sumatra area.

If Celebes had been the major center of evolution of *Calamaria*, one would expect to find many species, most of the morphological types, and at least several species in common with adjacent areas. The number (8) of species of *Calamaria* in Celebes is small compared to that of neighboring Borneo (21). Most of the morphological types are present (Table 63), but the absence of one—species having four supralabials—requires at least a subsidiary center of morphological radiation elsewhere. The only non-endemic Celebesian species is *C. virgulata*, which may be a composite of reproductively isolated forms (p. 187). Aside from the questionable taxonomy, *virgulata* does not provide evidence of a faunal source in Celebes, for it occurs in Mindanao, Palawan, Sumatra, and Java as well as Borneo and Celebes. It could not have spread directly from Celebes to all of these areas, whereas it could have reached them directly from Borneo.

On geological and zoogeographical grounds, Celebes is a poor site for the major center of evolution of *Calamaria*. The Makassar Strait, with channel depths exceeding 2000 meters, has separated Borneo and Celebes at least since the Eocene (Umbgrove, 1938). Given this circumstance fossorial forest snakes would have great difficulty dispersing between Borneo and Celebes. If Celebes had been the main center of evolution of *Calamaria,* only the limited possibilities of accidental dispersal could have carried stocks from this source to the main area of the generic range. Consequently, it would be necessary to assume a second center of radiation elsewhere, and in view of the many species in Borneo, the second center would be more important than a Celebes center.

The distribution of other snakes is also against locating the main center in Celebes. Celebes has 27 genera of non-marine snakes, 25 of them occurring in Borneo which has 47 genera (de Haas, 1950). Except for two endemics, the genera of Celebes snakes represent the results of sweepstakes migration (Simpson, 1940) across an ocean strait from Borneo. Darlington (1957) shows that the vertebrate fauna of Celebes is composed of groups that have moved in from adjacent areas.

Celebes nonetheless has been the site for a minor radiation of *Calamaria.* Seven of the eight species are endemic and, as noted above, most of the morphological trends taken by the genus appeared in these eight species. Probably no more than three stocks reached Celebes, a stock having unmodified teeth and one or two having modified dentition.

The Philippine Islands show little evidence of being an important center of evolution of *Calamaria.* The Tertiary and Pleistocene history of the Philippines is one of alternating periods of land emergence and subsidence (van Bemmelen, 1949), which should have favored fragmentation of populations and radiation. But the fauna is small (only 6 species) and several striking morphological types are absent (Table 63). Furthermore, the entire amphibian and reptilian fauna of the Philippines appears to have come from other areas and gives no evidence of a major faunal source in the Philippines (Inger, 1954).

Indo-China and China are not likely places for the center of radiation of *Calamaria.* They have only four species, lack most of the morphological types, and the contemporary climate is unfavorable. The last obstacle may not be a valid one, for the pre-Pleistocene climate was probably warmer and more humid (Dorf, 1959). If this area had been an important center of radiation, one should expect to find some representatives of less specialized *Calamaria* (e.g., species having five supralabials or unmodified maxillary teeth). This expectation is not fulfilled.

What remains of the range of *Calamaria* is Sundaland, the land masses of Borneo, Sumatra, Java, and Malaya. Throughout most of the Tertiary and during the glacial intervals of the Pleistocene, these areas (with the possible exception of Java) and much of the intervening South China Sea were areas of land emergence (Umbgrove, 1949). This vast region, which until very recent times was covered with tropical rain forest, has been an ideal area for the evolution of *Calamaria.* The presence of the great majority of species and of all the principal morphological types (Table 63) constitute sufficient evidence for that conclusion.

Given the intimate connections among the various parts of Sundaland, it may be superfluous to search for *the* center of radiation among them. However, as Java was apparently largely submerged during the Eocene, Miocene, and Pliocene (Umbgrove, 1949, figs. 47, 48, and 55), it probably could not provide the necessary environment over as long a period as Sumatra, Borneo, and Malaya. If Java has been an important area of morphological radiation of *Calamaria,* it has been so only since the Pliocene. As Java has only nine species of *Calamaria* and lacks several morphological types (Table 63) including the primitive ones having unmodified maxillary teeth, it is not a likely area of major radiation.

Malaya has been a relatively stable land mass through the Tertiary and Quaternary but has few species (6) of *Calamaria,* no endemic species, and lacks forms having unmodified maxillary teeth. Even if one assumes that the fauna of Malaya is poorly known—an assumption not supported by the large number (100) of species of non-marine snakes already reported from there (Tweedie, 1953)—the *Calamaria* fauna is not rich enough to suggest that Malaya was a major center of radiation.

Sumatra and Borneo remain as the contemporary land masses most likely to have been major centers of radiation or parts of a single major center. Both had large areas above sea level during most of the Tertiary and Quaternary (Umbgrove, 1949) and both have large assemblages of *Calamaria.* Sumatra has 16 species of which 10 are endemic (if Nias is included as part of a Sumatran area), and Borneo 21, of which 12 are endemic (if Cagayan Sulu may be included as part of Borneo). The Bornean species cover every principal morphological diversification of the genus (Table 63). The Sumatran assemblage lacks only species having four supralabials. All but one (*albiventer*) of the non-endemic species of Sumatra occur in Borneo and half of the non-endemics of Borneo are known from

Sumatra. The large proportion of endemics in each island indicates that each has probably been a center of radiation.

The preceding discussion has been more or less limited to present day land masses when perhaps it should not have been. Geologic evidence for a much more extensive land area in Sundaland during the Pleistocene (Molengraaff and Weber, 1921) and throughout most of the Tertiary (Umbgrove, 1949) is very strong. As the area between Borneo and Sumatra during periods of emergence would have been lowlands and covered with rain forest, it would have made an ideal habitat for *Calamaria.*

Probably it would be more correct to refer to one large central area of evolution comprising Borneo, Sumatra, and the now submerged inter-insular portion of Sundaland. This enlarged center, if at all important, had its main significance to radiation as a unit prior to Pleistocene times. During and after the Pleistocene, because of repeated inundation of the inter-insular region, this enlarged unit did not exist.

Evidence from species having wide ranges indicates that Sumatra and Borneo are not only centers of evolution but also centers of dispersal. Six species of *Calamaria* have distinctly larger ranges than the others. Two of them, *pavimentata* and *septentrionalis,* are restricted to the mainland of Asia and islands off the coast of China. The other four—*lumbricoidea, schlegeli, virgulata* and *modesta*—occur in Borneo and Sumatra, which are more or less centrally located in their ranges. These species could have spread to Malaya and Java from Sumatra or Borneo.

One species, *albiventer,* is known only from Sumatra and Malaya suggesting dispersal between those two areas. The presence of *lowi* in Malaya and Borneo suggests dispersal between those areas. The distribution of the uniform color variety of *lumbricoidea* (Table 21) also supports the latter route of exchange, probably during the Pleistocene (p. 267). The uniform color variety of *lumbricoidea* occurs in Borneo and Great Natuna among other places (Table 21) and has recently been collected on Tioman Island, 20 miles off the east coast of Malaya (Hendrickson, MS). As this color variety is not known from central or eastern Malaya (Table 21), its occurrence on Natuna and Tioman suggests a dispersal from Borneo westward toward Malaya or an origin in a pre-Recent land mass in what is now the South China Sea.

Probably *lumbricoidea* and *virgulata* spread to the Philippines from Borneo. In fact, all of the Philippine stocks of *Calamaria* came from Borneo. The Pleistocene drops in sea level caused by the formation of northern glaciers expanded land areas not only within Sundaland, but also between Sundaland and fringing areas. The gaps between the southern islands of the Philippines and Borneo were at least greatly narrowed if not temporarily obliterated. At those intervals the chances for successful dispersal from Borneo to the Philippines were increased considerably. Celebes can probably be ignored as a source for the Philippine *Calamaria* because the geologic evidence for land connection with the Philippines is weak (Umbgrove, 1938; van Bemmelen, 1949) and because the Celebes fauna is itself relatively impoverished. The one species common to the Philippines and Celebes is the dubious *C. virgulata;* it cannot be used as unequivocal evidence for Celebes-Philippines exchange since it could as well have reached both of those areas from Borneo. The mainland of Asia is not a likely source of the Philippine stocks because of the great distance and because the forms of *Calamaria* present in the closest parts of the mainland all have four supralabials, a character absent in the Philippine *Calamaria.* There is no evidence from other reptiles and amphibians of direct dispersal between southeastern Asia and the Philippines (Inger, 1954).

Because of the great age of the Makassar Strait between Borneo and Celebes (p. 275), species of *Calamaria* (or their ancestral stocks) could only reach Celebes by some means of accidental dispersal. The size of the Bornean fauna and its proximity to Celebes make it the logical source of the Celebes assemblage of *Calamaria.* Probably two or three stocks of *Calamaria* invaded Celebes (see above).

Time of dispersal and speciation.—Twenty-two species of *Calamaria* are endemic to either Borneo or Sumatra; only five species are known from both islands. Even granting that additional collecting will increase the number of species common to both islands, the ratio of endemic to common species probably will not change much. To assume otherwise implies that endemics are easier to find than nonendemics. If the collections available to us are any measure, the reverse is true. The average number of specimens seen of the 27 species found in either Borneo or Sumatra is 12; the average number seen of the five common to Borneo and Sumatra is 51.[1]

The preponderance of endemics in Borneo and Sumatra suggests that many of these species became distinct in the Pleistocene. Although we have no evidence for the date, it is reasonable to place the origin of the genus *Calamaria* at least in the Pliocene. This date makes the genus at least 5–13 million years old, depending on whether the origin is at the beginning or middle of the Pliocene. If the endemic species of *Calamaria* in these two islands date from the Pliocene, they are several million years old. Their failure to disperse between these islands in that length of time implies a slow rate of dispersal.

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[1] This average is based only on specimens collected in Borneo and Sumatra.

Some evidence concerning rates of dispersal of *Calamaria* can be obtained from the presence of species on certain islands. Nias is covered with Pliocene marine sediments (Umbgrove, 1949). Hence its three species, *C. lumbricoidea, abstrusa,* and *forcarti,* could not have arrived there prior to the Pleistocene. As all three occur in Sumatra, which had a large land surface throughout the Tertiary and Pleistocene, probably these three species invaded Nias from Sumatra during the Pleistocene. At present, relatively shallow water, i.e., less than 200 meters deep, extends from the northern tip of Nias to Sumatra (U. S. Hydrographic Office Chart 3122). This sixty-mile gap was at least very much narrowed if not completely obliterated several times during Pleistocene glacial stages. Though estimates of the length of the separate glacial stages vary, apparently none of these stages exceeded 100,000 years (Charlesworth, 1957; Dunbar, 1949). As some time was required for the ice to reach its maximum extent and, hence, to lower sea level to the maximum and as some time was required for forest to invade the new land, the maximum time available for overland migration of *Calamaria* from Sumatra to Nias was less than 100,000 years.

If three species, including widely distributed as well as restricted ones and representing 19 per cent (3/16) of the Sumatran fauna, could move 60 miles in less than 100,000 years, it is unreasonable to assume that only 5 of 32 species (the total *Calamaria* fauna of Borneo and Sumatra) could disperse across an area three and one-half times as wide as the Nias channel in more than one million years of pre-Pleistocene time. Consequently, we think that the argument for a very slow rate of dispersal, on which a pre-Pleistocene origin for most of the Sumatran and Bornean endemics depends, is weak. The alternative suggestion of a Pleistocene origin for many of these endemics seems to be in accord with more of the known geological and zoogeographical facts.

The relatively rapid rate of evolution suggested for these snakes is paralleled by the rate attained by the endemic cyprinid fishes of Lake Lanao, Mindanao. Myers (1960) estimates that the 13 species in the lake evolved in little more than 10,000 years from a single species, *Puntius binotatus,* that reached Mindanao from North Borneo during the Pleistocene.

That many forms of *Calamaria* apparently evolved during the Pleistocene in one or two parts of the range does not prove that the same is true in all areas. The Celebesian species may have developed during the same time. At least the Pleistocene was a favorable interval for the genus to disperse to Celebes from Borneo. If the three Philippine species, *gervaisi, bitorques,* and *joloensis,* or their ancestral stock reached that area during the Pleistocene and differentiated then, their similarity to the Celebes species *muelleri* would be understandable in terms of a relatively recent origin.

The northern limit of warm temperate forest in eastern and southeastern Asia at the height of the last glaciation was at about 27° N (Charlesworth, 1957, fig. 293), or only a few degrees south of its postglacial boundary. The continental forms of *Calamaria* could, therefore, have occupied their present ranges during the Pleistocene or even earlier, since the climate of the Pliocene was milder than that of the Quarternary (Dorf, 1959).

SUMMARY

Calamaria is a highly successful member of a group of fossorial colubrid genera that form a characteristic part of the snake fauna of the Indo-Malayan tropical forests. Although all of these genera have lost or consolidated some of the head scales, reduced the number of scale rows, and strengthened the side of the snout in a distinctive way, *Calamaria* is one of the most specialized within the group.

Whether because of its greater specialization or for other reasons, *Calamaria* appears to be the most successful of these calamarine genera. It has far more species (50) than all of the other genera combined and its geographic range is more extensive than the combined ranges of the other genera.

Various levels of specialization are evident within the genus *Calamaria*. Most of the species have laterally compressed, flask-shaped maxillary teeth; this modification is accompanied by a deepening of the maxilla. Some species have reduced the supralabials to four; some have lost the preocular; others have extremely short tails; others have become extremely slender. The specializations in the various characters appear in almost all possible combinations.

These combinations are evidence of a remarkable amount of parallelism. Apparently many stocks have had the capacity to evolve in several directions. Another element in the pattern of evolution of this genus is the importance of variable species, which, though relatively generalized, have had a balance among mutation, response to selection, inbreeding, and gene flow that has enabled them to evolve rapidly and proliferate new forms.

Both extrinsic and intrinsic factors have played a role in the evolution within the genus. The periodic fragmentation of the heart of the range during the Pleistocene provided opportunities for the development of reproductive isolation. The tendency toward local differentiation seen in many species and reflecting a rapid rate of genetic change led to the development of genetic isolation and speciation. Most of the evidence now available suggests that many species, perhaps as large a proportion as one-half, differentiated during Pleistocene or post-Pleistocene times.

Though the generic range extends from eastern China and Burma to Ceram, Celebes, and the Philippine Islands, the majority of species (64%) of *Calamaria* occur in Sumatra and Borneo. Because of the large proportion of the species found on these islands and because of the geological stability of these islands during most of the Tertiary and Quaternary, they were probably the principal centers of evolution and dispersal of the genus.

APPENDIX A

FORMATION OF DENDROGRAM

The method used in constructing the dendrogram of phenetic relations is based on mean character difference (Cain and Harrison, 1960). Fourteen characters were used: number of supralabials, number of scales surrounding the paraparietal; the relationship between mental and chin shields; presence or absence of preocular; dorsal scales with or without pigment network; light stripe on first or second scale row bounded above and below by dark pigment; light spots or bars on the sides opposite the vent; number of maxillary teeth; position of the reduction to four scale rows on the tail; number of ventrals; number of subcaudals; sex dimorphism in ventral counts; sex dimorphism in subcaudal counts; and body thickness. The characters are described in the introduction (pp. 14–50).

For the purposes of comparing species, the first seven characters were scored as follows:

CHARACTER	STATE	SCORE
supralabials	four	0
”	five	100
paraparietal surrounded by	five scales	0
”	six scales	100
mental and chin shields	separated	0
”	touching	100
preocular	absent	0
”	present	100
dorsal scale pigment network	absent	0
”	present	100
light, dark-edged stripe	absent	0
”	present	100
light spots opposite vent	absent	0
”	present	100

TABLE 64.—Character Scores Used in Calculating Mean Character Differences Between Species of *Calamaria.*

	Supralabials	Paraparietals	Mental	Preocular	Teeth	Reduction	Ventrals	Subcaudals	Sex dimorphism ventrals	Sex dimorphism subcaudals	Girth	Color		
												Dorsal scales with network	Light stripe on first scale row	Light spots, bars, rings at vent
lumbricoidea	100	0	100	100	100	29	28	27	47	12	42	0	0	0
griswoldi	100	0	100	100	91	63	26	16	53	7	37	0	0	0
albiventer	100	0	100	100	67	75	9	29	42	10	..	0	0	0
hilleniusi	100	0	100	100	100	44	12	20	0	5	56	0	0	0
muelleri	100	0	100	100	33	29	13	16	68	18	38	100	0	0
joloensis	100	0	100	100	33	35	..	..	..	..	..	100	0	0
bitorques	100	0	100	100	67	55	18	22	58	13	49	100	0	0
gervaisi	100	0	100	100	52	40	14	11	47	12	23	100	50	0
brongersmai	100	0	0	100	33	21	13	9	0	25	..	100	0	0
suluensis	100	0	100	100	16	69	4	29	63	0	..	100	100	0
prakkei	100	0	100	100	5	61	0	100	53	10	..	100	100	0
everetti	100	0	0	100	67	99	6	38	0	0	..	100	100	0
palavanensis	100	0	0	100	67	47	24	38	21	13	23	100	100	0
grabowskyi	100	0	100	100	60	100	24	53	21	5	30	100	100	0
modesta	100	50	0	100	22	21	23	40	58	21	35	50	50	0
lateralis	100	0	0	100	33	78	5	33	11	14	..	0	0	0
lumholtzi	100	0	0	50	33	43	..	..	..	..	..	0	0	0
bicolor	100	0	0	100	76	56	11	42	21	12	50	0	50	0
schlegeli	100	50	0	50	77	79	11	73	63	9	21	0	0	0
margaritophora	100	100	100	100	50	34	12	0	0	19	53	100	100	0
nuchalis	100	100	100	100	89	49	5	4	53	39	..	100	100	0
crassa	100	100	100	100	100	31	11	36	53	28	51	100	0	0
eiselti	100	100	100	100	100	47	5	7	47	100	86	100	0	0

TABLE 64.—Character Scores Used in Calculating Mean Character Differences Between Species of *Calamaria* (Cont.)

												Color		
	Supralabials	Paraparietals	Mental	Preocular	Teeth	Reduction	Ventrals	Subcaudals	Sex dimorphism ventrals	Sex dimorphism subcaudals	Girth	Dorsal scales with network	Light stripe on first scale row	Light spots, bars, rings at vent
doderleini	100	100	0	100	100	35	. .	. .	. .	. .	. .	100	0	0
abstrusa	100	100	100	100	58	29	4	29	47	28	. .	0	0	0
boesemani	100	100	0	100	67	35	. .	. .	. .	. .	. .	0	0	0
sumatrana	100	100	100	100	50	23	14	11	79	19	. .	100	100	100
virgulata	100	50	50	100	67	24	43	11	53	28	10	100	100	50
forcarti	100	100	100	100	33	56	32	47	53	32	. .	100	0	100
borneensis	0	100	100	100	51	34	18	33	58	9	32	100	50	0
melanota	0	100	100	100	61	33	1	38	42	13	. .	100	0	0
linnaei	0	100	100	100	100	26	4	7	58	31	100	100	0	0
javanica	0	100	100	0	50	28	23	4	16	17	. .	100	0	0
buchi	0	0	100	100	67	15	. .	. .	. .	. .	17	100	0	50
pavimentata	0	50	0	100	57	25	16	27	53	18	. .	100	50	100
septentrionalis	0	100	0	100	40	0	19	2	63	34	56	100	100	50
lowi	0	100	50	0	69	22	50	20	74	20	0	0	0	50
gracillima	0	100	0	0	100	29	100	2	0	8	. .	0	0	100
rebentischi	100	0	0	0	0	6	. .	. .	. .	. .	. .	100	100	0
ceramensis	100	0	0	0	27	28	6	51	37	16	41	100	100	0
mecheli	100	100	0	0	56	12	7	38	37	39	. .	100	100	50
alidae	100	100	50	0	67	19	48	36	100	16	. .	100	50	50
apraeocularis	100	100	100	0	56	16	41	7	95	33	. .	100	0	0
battersbyi	0	100	100	100	33	18	. .	. .	. .	. .	. .	0	. .	100

If a species showed geographic variation in one of these seven characters (e.g., *schlegeli* in preocular and *virgulata* in the mental shield character) or extensive individual variation (e.g., *C. gervaisi* in the light stripe), it received a score of 50 for that character.

For the remaining seven characters, we used a slight modification of the method outlined by Cain and Harrison (1960), who simply set the highest value of a given character in a suite of species equal to 100 and scored all other values of that character as decimals of the highest. In the case of average number of ventrals, which ranges from 136 to 296, the lowest score for any species is .46.[1] Thus the maximum possible interspecific difference in ventral counts would be 54. As the maximum possible interspecific difference is 100 in the first seven characters, this procedure would give greater weight to each of those characters than to the ventrals. But the reason for undertaking this numerical approach was our inability to justify weighting these characters. To avoid introducing bias, we subtracted the smallest average ventral count (136) from all of the averages, thus arriving at a zero value for at least one species. The maximum interspecific difference in ventral counts then reached 100.

We made a similar subtraction in the following characters: subcaudal counts, reduction to four scale rows, percentage of sex dimorphism in ventral and subcaudal counts, number of maxillary teeth, and body thickness.

To obtain the average of ventral counts for a given species, we added the means for males and females and divided by 2. This procedure gives equal weight to both sexes. Subcaudal counts were treated the same way.

For sex dimorphism in ventrals, we divided the difference between the means of males and females by the mean of males for the particular species. This procedure gave sex dimorphism in ventrals as a percentage of the average male count (generally the smaller of the two means). Sex dimorphism in subcaudal counts was determined the same way except that the base was the mean female count, which is the lower mean.

If only one sex was available for a species, ventral and subcaudal counts and sex dimorphism were not used in comparing that species with others.

The value for thickness of each species was derived from the mean of those specimens in the size range 300–399 mm. Because relative thickness increases with increasing size, we felt it necessary to eliminate juveniles as well as extremely long specimens (i.e., greater than 400 mm.), which occur in only four species.

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[1] In actual practice, we multiplied this score by 100 in order to avoid the decimal points. That practice is assumed for the rest of this discussion.

The character values for the 44 species having modified maxillary teeth are given in Table 64. From this set, we calculated the matrix of mean character differences presented in Table 60.

Certain characters used in our "quantitative" analysis of interspecific similarity have a continuous pattern of variation. Ventrals, subcaudals, reduction, and sex dimorphism in ventrals and subcaudals are apparently under multigenic control such that a change in any part of the genetic background causes a small recorded change in the value of the character.

For example, in the percentage evaluation of characters, the character "reduction" has values at all levels between 0 and 100. Within a species, variation in this character proceeds in small steps relative to the total range of the character in the genus (see Table 46). The mean value for the species *schlegeli* is 13.5. A slight change in the mean is possible and would result in only a slight change in the percentage value in Table 64. Similar comments could be made of the characters mentioned above.

The pattern of variation in other characters used in our analysis is radically different. "Presence or absence" characters vary or their variations are recorded in relatively large steps. The number of scales around the paraparietal is either 5 or 6; the number of supralabials is either 4 or 5. Although one must assume that these characters also are controlled by many genes, a change in any part of their genetic background causes either a large recorded, relative change in the character or none at all. Changes at either end of the scale are thus magnified resulting in many interspecific differences of high or low magnitude.

The technique of estimating similarity by use of mean character differences works without bias if the pattern of variation is approximately the same for each character. Sneath (1961) uses 14 body proportions to illustrate two methods of analysis. As body dimensions vary continuously and as their minor variations are recorded as well as the major ones, the patterns of variation of body proportions are similar.

If differences between species in these two general kinds of characters are lumped together in calculating mean character differences, bias might be introduced. However, by using equal numbers of both kinds of characters, except in seven species, we believe we have minimized this danger. After removal of the seven species for which we have inadequate data, estimates of mean character differences between *lumbricoidea* and the remaining species, based upon the two sets of characters, are reasonably close in the species most similar to *lumbricoidea.* If a joint estimate of 30 is used as the cut-off point—and our dendrogram analysis gives us little confidence in mean character differences beyond that level—the two separate estimates of that mean differ by 5 or less in 9 of 18 comparisons and exceed 15 in only 6 of the 18.

Having satisfied ourselves, at least, that the method of scoring characters did not introduce a bias, we made a dendrogram (Fig. 67) of phenetic relations based on the mean character differences ("m.c.d.," the abbreviation used by Cain and Harrison, is adopted in the following discussion) in Table 60. The method is similar to the unweighted variable group method described by Sokal and Michener (1958) for use with correlations. Each species was joined to that one with which it had the lowest m.c.d. unless the second one had a lower m.c.d. with a third species. In that event the first species was usually joined to the group formed by the second and third. For example, *albiventer* and *griswoldi* have an m.c.d. of 6.2. But *griswoldi* and *lumbricoidea* have an m.c.d. of 5.1, the lowest m.c.d. in which either is involved. The nucleus of a group is formed by the last two and *albiventer* is joined to that group.

Two species were always paired as the nucleus of a group if their m.c.d. with one another was lower than the m.c.d.'s of each with all other species. There were eleven such pairs: *lumbricoidea-griswoldi, margaritophora-nuchalis, everetti-palavanensis, muelleri-joloensis, suluensis-prakkei, lateralis-lumholtzi, rebentischi-ceramensis, apraeocularis-alidae, melanota-borneensis, pavimentata-septentrionalis,* and *lowi-gracillima.* One triad of species, *crassa, eiselti,* and *doderleini,* had such similar m.c.d.'s (11.6, 11.7, 12.4) that they formed the nucleus of a group.

In adding a species to a group the average of its m.c.d.'s with all the members of the group determined the level of its connection. For example, in joining *gervaisi* to the group *muelleri-joloensis-bitorques,* the average (8.9) of its three m.c.d.'s (8.2, 9.1, 9.5) with those three species gave the level of the connection. In combining groups, the m.c.d.'s of the members of one with all members of the other were used to arrive at a mean m.c.d. Thus to determine the level at which the *prakkei-suluensis* group joined the *muelleri-joloensis-bitorques-gervaisi* cluster required the average of eight m.c.d.'s.

Some situations did not fit the simple logic of this outline. *Calamaria grabowskyi* has the same m.c.d. (12.8) with *suluensis* as with *everetti*, each of which has a lower m.c.d. with another species. The m.c.d. (19.8) of *suluensis* and *everetti* is moderately high. The average m.c.d. of *grabowskyi* with the nucleus group *everetti-palavanensis* is lower than that with *suluensis-prakkei; grabowskyi* was therefore attached to the former group.

Some species or groups of species had equivalent average m.c.d.'s to a third group but much higher m.c.d.'s with each other. For example, *brongersmai* had an average m.c.d. with the *muelleri-joloensis-bitorques-gervaisi* group of 16.6; the mean m.c.d. of *prakkei-suluensis* with the *muelleri* group was 17.3; the mean m.c.d. of *brongersmai* with *prakkei-suluensis* was 31.6. If we followed the logic of the method rigorously, *brongersmai* should be included in the *muelleri* group and the m.c.d. of the enlarged *muelleri* group to *prakkei-suluensis* recalculated. This procedure would lower the level at which the last two groups join and would obscure the similarity of *prakkei-suluensis* to the restricted *muelleri* group.

Inclusion of *brongersmai* in the *muelleri* group and recalculation of the m.c.d.'s of the latter with all other groups would in every instance lower the level of the connection between groups. One interpretation of this situation is that the similarity of *brongersmai* to the *muelleri* group results from parallelism; another is that *brongersmai* is an off-shoot of the *muelleri* stock that developed after the latter split off from the other stocks. Our guess is that the first explanation is more nearly correct. At any rate, in order not to obscure the similarity of the *muelleri* group to the others, we arbitrarily did not include *brongersmai* in it though the dendrogram shows the level of its similarity to the *muelleri* group.

Calamaria modesta caused a similar problem that was handled in the same way. The solid line indicates the level of its similarity to the *grabowskyi-everetti-palavanensis* group and the dashed line the level of its similarity to *palavanensis*.

Several alternative ways of connecting groups in the dendrogram were possible. These are indicated by dashed lines. The solid lines indicate the connections that gave the lowest m.c.d.'s over all.

Appendix B: Faunal List

- AMBON
  - _ceramensis_
- AOR
  - _lowi_
- BALI
  - _schlegeli_
- BANGKA
  - _schlegeli_
- BASILAN
  - _gervaisi_
  - _lumbricoidea_
- BILLITON
  - _javanica_
  - _schlegeli_
- BOHOL
  - _lumbricoidea_
- BORNEO
  - _battersbyi*_
  - _bicolor_
  - _borneensis*_
  - _everetti*_
  - _grabowskyi*_
  - _gracillima*_
  - _griswoldi*_
  - _hilleniusi*_
  - _lateralis_
  - _leucogaster_
  - _lowi_
  - _lumbricoidea_
  - _lumholtzi*_
  - _melanota*_
  - _modesta_
  - _prakkei_
  - _rebentischi*_
  - _schlegeli_
  - _schmidti*_
  - _suluensis_
  - _virgulata_

* endemic

- BURMA
  - _pavimentata_
- CAGAYAN SULU
  - _suluensis_
- CELEBES
  - _acutirostris*_
  - _apraeocularis*_
  - _boesemani*_
  - _brongersmai*_
  - _curta*_
  - _muelleri*_
  - _nuchalis*_
  - _virgulata_
- CERAM
  - _ceramensis_
- CHINA
  - _pavimentata_
  - _septentrionalis_
- COCOS ISLANDS
  - _lautensis*_
- FORMOSA
  - _pavimentata_
- GREAT NATUNA
  - _lumbricoidea_
- HAINAN
  - _septentrionalis_
- HONG KONG
  - _septentrionalis_
- INDO-CHINA
  - _buchi*_
  - _pavimentata_
  - _septentrionalis_
- JAVA
  - _bicolor_
  - _javanica_
  - _lateralis_
  - _linnaei_
  - _lowi_
  - _lumbricoidea_
  - _modesta_
  - _schlegeli_
  - _virgulata_
- JOLO
  - _?gervaisi_
  - _joloensis*_
- LEYTE
  - _lumbricoidea_
- LUZON
  - _bitorques*_
  - _gervaisi_
- MALAYA
  - _albiventer_
  - _lowi_
  - _lumbricoidea_
  - _pavimentata_
  - _prakkei_
  - _schlegeli_
- MINDANAO
  - _gervaisi_
  - _lumbricoidea_
  - _virgulata_
- MINDORO
  - _gervaisi_
- NEGROS
  - _gervaisi_
  - _lumbricoidea_
- NIAS
  - _abstrusa_
  - _forcarti_
  - _lumbricoidea_
- PALAWAN
  - _palavanensis*_
  - _virgulata_

PANAY
gervaisi

POLILLO
gervaisi

RIOUW ARCHIPELAGO
lowi

RIU KIU ISLANDS
pavimentata

SAMAR
lumbricoidea

SAPARUA
ceramensis

SIMALUR
modesta

SULU ARCHIPELAGO
virgulata

SUMATRA
abstrusa
albiventer
*alidae**
*crassa**
*doderleini**
*eiselti**
forcarti
leucogaster
lumbricoidea
*margaritophora**
*mecheli**
modesta
schlegeli
*sumatrana**
*ulmeri**
virgulata

TABLAS
gervaisi

THAILAND
lumbricoidea

* endemic

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